# Ecosystem Carbon Dynamics
# in
# Logged Forest of Malaysian Borneo

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**Universität Zürich**

von

**Philippe Gérard Saner**

aus

**Beinwil (SO)**

**Promotionskomitee:**

Prof. Dr. Andrew Hector (Leitung der Dissertation)

Prof. Dr. Bernhard Schmid

Prof. Dr. Michael Scherer-Lorenzen

Dr. Simon Egli

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# Contents

# 1 Summary

The tropical rainforest of Borneo is heavily disturbed by logging, to date less than half of the original forest cover remains. To counteract such development logged forest is rehabilitated to regenerate its natural protective function. In this thesis we consider the carbon budget of logged forest and the ecology of the trees that are planted for rehabilitation. We show that the logged forest under study differs from unlogged forest due to the lack of the dominant trees and hence the organic carbon that is stored in their biomass. Besides this difference our results indicate that logged forest can maintain its protective function for carbon storage and is therefore worth preserving. The dominant trees, known as dipterocarps, belong to the Dipterocarpaceae family and are keystone species of the lowland forests of Borneo. On the basis of experimental work we study the carbon dynamics of selected dipterocarp species at the seedling stage. With plant physiological measurements of the carbohydrate stores we demonstrate how seedlings adapt to a changing light environment. Our results show that photosynthates are invested into growth or carbohydrate reserves, irrespective of the tree species under study. Further, experimental evidence suggests that the ectomycorrhizal association (plant-fungi-symbiosis) is crucial for the growth of seedlings and should therefore be considered for forest rehabilitation measures. In contrast we could not find evidence for a complex ectomycorrhiza-network between dipterocarp trees and seedlings in logged forest.

In Chapter 1 we describe the study area in the logged forest with regard to environmental factors that are relevant for forest rehabilitation. We address the intensity of previous forest exploitation, age and composition of the existing forest stand, soil specification and climatic conditions. This is the first comprehensive description of the logged forest of the Sabah Biodiversity Experiment, a large scale forest rehabilitation project in North-East Borneo.

In Chapter 2 we present a carbon balance for the logged forest of the Sabah Biodiversity Experiment. We quantify the six main carbon sinks: above-ground tree biomass, above-ground non tree biomass, below-ground root biomass, litter, dead wood and soil. In particular the above-ground tree biomass is an

important carbon sink. In comparison to unlogged forest the bound tree carbon in logged forest is lower. This can be explained with the lack of big trees (>90 cm diameter at breast height) of the Dipterocarpaceae family. Based on these results we conclude that forest rehabilitation measures are essential to regain the carbon sink potential of the tree biomass in logged forest. In addition we compare tree diversity in logged forest compared to pristine forest and find that the level of diversity (Fisher's $\alpha$) is similar higher in logged forest. Once we consider tree species composition in logged forest, we find that the forest stand is defined as heavily degraded secondary forest. In contrast the quantity in standing dead wood, fine root biomass and litterfall rates, which all represent indicators for nutrient- and carbon dynamics, indicate a less degraded system. All three indicators are similar in logged and unlogged forest, suggesting that a logged forest can fully maintain these ecosystem processes.

In Chapter 3 we study to what extend forest stand structure and composition alters the soil respiration rate. Soil respiration is one of the most relevant quantities to be measured in a carbon budget. It represents the direct exchange of carbon dioxide ($CO_2$) between the forest floor and the atmosphere. Our results illustrate that soil respiration rates are significantly lower in forest canopy gaps, but do not change between different forest stands.We identify a higher soil temperature and a lower litterfall input as the driving factors. Our results show that soil respiration rates during the night decrease by about one fifth compared to day rates. Despite the fact that our results indicate a major contribution of root respiration to total soil respiration, we could not find a direct relationship between stand diameter and soil respiration rate.

In Chapter 4 we consider the carbon balance on the level of individual trees. In a shadehouse experiment we test for the importance of changing light environments on the growth and carbohydrate storage of dipterocarp seedlings. It is generally known that seedlings grown in the understorey of a tropical forest are light limited. An overthrown tree or a broken off branch can result in a canopy gap and increased light conditions that allow a seedling to grow. As the competition between seedlings is high, we expect that they

pursue different survival strategies. We simulate the creation and closure of canopy gaps to test, whether seedlings that experience a sudden light change will invest photosynthates into instant growth or into stores for later survival. In five out of six species we find that an increased growth is negatively correlated with the amount of stored carbohydrates. In addition we identify a yet unknown component of carbohydrate stores in dipterocarp trees. Iditol–a sugar alcohol–contributes up to half of the stored carbohydrates, depending on species and the light environment under study.

In Chapter 5 we study the influence of light, nutrients and ectomycorrhiza (plant-fungi-symbiosis) on the growth of *Vatica albramis* (Dipterocarpaceae) seedlings. We hypothesise that it is more advantageous to plants to trade carbon for nutrients with ectomycorrhiza under low light than hight light. We test this by relating the ectomycorrhizal benefit to the plant with an increase in relative mass growth, where we expect that the growth is higher when light conditions and carbohydrate supply is higher. In forest rehabilitation projects seedlings are raised in the nursery before they are outplanted. The soil used to raise the seedlings is typically excavated forest subsoil that is dried for one week prior to shredding. We expect that soil drying lowers the naturally occuring hyphae and spores of ectomycorrhiza which may negatively affect plant growth. We treat soil in our experiments with the same method of soil solarization and show that reducing the ectomycorrhiza symbionts can reduce seedling growth for up to one year.

In Chapter 6 we use the existing logged forest of the Sabah Biodiversity Experiment and the remaining adult Dipterocarpaceae of the area. Seedlings of *Dryobalanops lanceolata* and *Shorea parvifolia* are planted under an adult tree of the same and of the other species. We expect that an ectomycorrhizal network may support seedlings that grow under sub-optimal light conditions, as they may receive carbohydrates from the adult dipterocarp tree. Our results cannot support this assumption. Seedlings of both species grow better in close proximity to adult *Dryobalanops lanceolata* trees, however this effect is not related to an ectomycorrhizal network. It is possible that *Dryobalanops lanceolata* trees appear in locations that are

beneficial to the growth of seedlings, or that carbohydrates of the adult trees of this species are present at higher concentrations in the surrounding soil and are absorbed by the seedlings outside the proposed hyphal network.

In the General Discussion we present a carbon budget for the reported values of chapter 2 and 3. This can be used as a foundation for future measurements of logged forest productivity of the Sabah Biodiversity Experiment. We understand productivity as an increase in biomass over time, which can be related to an increase in stored organic carbon. The productivity of the forest is not directly determined here, however we recognize that this should be part of future research activity in this area. For chapter 4, 5 and 6 we put our results into context with current theories of tree guild coexistence in tropical forests. We understand a guild as a group of dipterocarp species which adapt their growth to changes in the light conditions and ectomycorrhizal infection in similar ways. We conclude that the experimental work presented here advances our knowledge on potential niche axes of selected dipterocarp species which is needed to test whether random (neutral) processes can explain tree species diversity in tropical forests.

# 2 Zusammenfassung

Die tropischen Regenwälder Borneos sind durch Abholzung gekennzeichnet, weniger als die Hälfte der ursprünglichen Fläche ist noch bewaldet. Um dieser Entwicklung entgegenzuwirken, können gerodete Wälder durch Aufforstungsmassnahmen gezielt regeneriert und die Produktivität und natürliche Schutzfunktionen des Waldes wiederhergestellt werden. Wir befassen uns in dieser Arbeit mit dem Kohlenstoffhaushalt des gerodeten Waldes und der Ökologie der Bäume die für die Aufforstung verwendet werden. Die Messeinheit ist der in der Biomasse gebundene organische Kohlenstoff. Unsere Resultate deuten darauf hin, dass auch gerodeter Wald natürliche Schutzfunktionen bietet und somit erhaltenswert ist. Wir zeigen, dass sich der Kohlenstoffhaushalt im gerodeten Wald vor allem durch das Fehlen der grossen Bäume von ursprünglichem Wald unterscheidet und Aufforstungsmassnahmen deshalb notwendig sind. Die dominanten Bäume gehören zur Familie der Flügelfruchtgewächse (Dipterocarpaceae) und gelten als Leitart der bornesischen Tieflandregenwälder. Anhand von Experimenten mit Setzlingen dieser Baumfamilie zeigen wir, dass sich Dynamiken im Kohlenstoffhaushalt eines Waldes auf der Ebene einzelner Pflanzen messen lassen. Mit Hilfe von pflanzenphysiologischen Messungen der Kohlenhydratspeicher demonstrieren wir wie sich Setzlinge an veränderte Lichtbedingungen anpassen. Wir finden heraus, dass sie Photosyntheseprodukte artunabhängig entweder in Wachstum oder in Speicherung investieren. Des Weiteren zeigen unsere experimentellen Versuche, dass die Assoziation mit Ektomykorrhizen (Pflanzen-Pilz-Symbiose) entscheidend ist für das Wachstum der Setzlinge und somit bei Aufforstungsprojekten beachtet werden sollte. Im Gegensatz dazu können wir keine Indizien für ein komplexes Ektomykorrhizen-Netzwerk zwischen Bäumen im Wald finden.

In Kapitel 1 beschreiben wir das Studiengebiet im gerodeten Wald in Bezug auf Umweltfaktoren die für Aufforstungsmassnahmen relevant sind. Dies sind insbesondere die Intensität der kommerziellen Nutzung des Waldes vor der Aufforstung, Alter und Zusammensetzung des Baumbestandes, Bodenbeschaf-

fenheit und klimatische Bedingungen. Dies ist die erste umfassende Beschreibung des Sabah Biodiversität Experimentes, eines gross angelegten Aufforstungsprojektes im Nordosten Borneos.

In Kapitel 2 präsentieren wir eine Kohlenstoff Bilanz für das Sabah Biodiversität Experiment. Dabei quantifizieren wir sechs wichtige Kohlenstoff-Senken: die oberirdische Biomasse der Bäume, sonstige oberirdische Biomasse, unterirdische Wurzelbiomasse, Laubschicht, Totholz und Boden. Vor allem die oberirdische Biomasse der Bäume ist eine wichtige Kohlenstoffsenke. Im Vergleich zu ursprünglichem Wald ist der gebundene Kohlenstoff im gerodeten Wald kleiner. Dies erklärt sich durch das Fehlen der grossen Bäume (>90 cm Umfang auf Brusthöhe), unter anderem aus der Familie der Flügelfruchtgewächse. Basierend auf diesen Resultaten kommen wir zum Schluss, dass Aufforstungsmassnahmen notwenig sind um das Kohlenstoff-Senkenpotential der Baumbiomasse wieder herzustellen. Im Weiteren vergleichen wir die Baumdiversität in gerodetem Wald mit ursprünglichem Wald. Unsere Resultate zeigen, dass die Baumdiversität (Fisher's $\alpha$) im gerodeten Wald nicht signifikant kleiner ist als im ursprünglichen Wald. Wenn nun aber die Artzusammensetzung in gerodetem Wald genauer betrachtet wird, finden wir dass der Baumbestand als schwer geschädigter Sekundärwald definiert wird. Im Gegensatz dazu zeigen Messungen von stehendem Totholz, Feinwurzelbiomasse und Laubfallraten, welche als Indikatoren für Nährstoff und Kohlenstoffumsatzraten gelten, ein anderes Bild. Alle drei Indikatoren sind vergleichbar zwischen gerodetem und ungestörtem Wald, dies deutet darauf hin, dass der gerodete Wald diese Ökosystemprozesse vollumfänglich unterstützt.

In Kapitel 3 untersuchen wir, inwiefern die Waldstruktur und die Zusammensetzung des Baumbestandes die Bodenatmungsrate beeinflussen. Bodenatmung ist eine der wichtigsten Grössen im Kohlenstoffhaushalt des Waldes und führt zum direkten Austausch von Kohlendioxid ($CO_2$) zwischen dem Boden und der Atmosphäre. Unsere Resultate zeigen dass die Bodenatmungsrate in Waldlücken kleiner ist, aber nicht von der Zusammensetzung des Baumbestandes abhängt. Wir identifizieren eine höhe-

re Bodentemperatur und einen niedrigeren Laubfalleintrag als die Wichtigsten erklärenden Variablen. Unsere Resultate zeigen zudem, dass die Bodenatmungsraten in der Nacht rund ein Fünftel unter den Tageswerten liegen. Obwohl die Resultate darauf hindeuten, dass Wurzelatmung eine wichtige Komponente der Bodenatmung ist, können wir keinen direkten Zusammenhang zwischen Baumumfang und Bodenatmung finden.

In Kapitel 4 befassen wir uns mit dem Kohlenstoffhaushalt aus der Sicht des einzelnen Baumes. In experimentell angelegten Schattenhäusern untersuchen wir den Einfluss von sich ändernden Lichtbedingungen auf den Wachstum und den Kohlenhydratspeicher von Setzlingen der Flügelfruchtgewächse. Es ist generell bekannt, dass die Setzlinge im Unterwuchs des tropischen Regenwaldes Licht limitiert sind. Ein umgestürzter Baum oder ein abgebrochener Ast können eine Lücke im Laubdach entstehen lassen, welche dem Setzling ermöglicht aus dem Unterwuchs herauszuwachsen. Da der Konkurrenzdruck zwischen den einzelnen Setzlingen gross ist, erwarten wir, dass sie unterschiedliche Überlebensstrategien verfolgen. Wir simulieren die Entstehung und das Zuwachsen von Lücken im Laubdach um zu testen, ob Setzlinge – welche einer plötzlichen Lichtänderung ausgesetzt werden – ihre Photosyntheseprodukte in sofortiges Wachstum oder in Speicherung für späteres Überleben investieren. In fünf von sechs untersuchten Arten können wir nachweisen, dass ein grösseres Wachstum negativ korreliert mit der Menge an gespeicherten Kohlenhydraten. Zudem identifizieren wir eine Kohlenhydratkomponente in Flügelfruchtgewächsen die bis anhin unbekannt war in tropischen Bäumen. Iditol – ein Zuckeralkohol – macht abhängig von der untersuchten Art und Lichtbedingung bis zur Hälfte des Kohlenhydratspeichers der Setzlinge aus.

In Kapitel 5 untersuchen wir den Einfluss von Licht, Nährstoffen und Ektomykorrhizen (Pflanzen-Pilz-Symbiose) auf den Wachstum von *Vatica albramis* (Dipterocarpaceae) Setzlingen. Unsere Hypothese beruht auf der Annahme dass Pflanzen gespeicherten Kohlenstoff mit Ektomykorrhizen gegen Nährstoffe eintauschen und dass der Nutzen dieses Austausches lichtabhängig ist. Wir beziehen den Nutzen der

Ektomykorrhizen Symbiose auf den erhöhten Wachstum der Setzlinge und erwarten dass dieser positiv korreliert mit erhöhten Lichtbedingungen und daraus resultierenden vorhandenen Kohlenhydraten. Wir erwarten, dass Setzlinge in dunklen Lichtbedingungen entweder in Wachstum oder in die Symbiose mit Ektomykorrhizen investieren. Die Ergebnisse verwerfen unsere Hypothese, da die Korrelation zwischen Pflanzenwachstum und ektomykorrhizierten Wurzelspitzen auch in dunklen Bedingungen positiv ist. Wir vermuten deshalb, dass die untersuchten Setzlinge die symbiotische Beziehung nur begrenzt Nutzen können, da diese unabhängig ist vom relativen Wert der ausgetauschten Kohlenhydrate.

In Aufforstungsprojekten werden Setzlinge zuerst in Baumschulen angezogen und danach angepflanzt. Die Erde, welche benutzt wird um die Setzlinge anzuziehen, wird üblicherweise im Wald ausgebaggert und danach für mindestens eine Woche getrocknet. Dies ist notwendig da die Erde sehr lehmig ist und ansonsten nur mühsam zerkleinert werden kann. Wir erwarten, dass diese Methode die natürlich vorkommenden Hyphen und Sporen der symbiotischen Ektomykorrhizen in der Erde abtötet, was sich negativ auf das Pflanzenwachstum auswirken kann. Wir behandeln die Erde in unserem Experiment mit der gleichen Methode und zeigen, dass das Abtöten der Ektomykorrhizen den Wachstum der Setzlinge bis zu einem Jahr verringert.

In Kapitel 6 benutzen wir das Waldgebiet des Sabah Biodiversität Experimentes und der darin vorkommenden Flügelfruchtgewächse. Setzlinge von *Dryobalanops lanceolata* und *Shorea parvifolia* wurden jeweils unter adulten Bäumen der eigenen oder der anderen Art gepflanzt. Wir vermuten dass ein Ektomykorrhizen-Netzwerk zwischen den adulten Bäumen und den Setzlingen dazu führt, dass die Setzlinge unter sub-optimalen Lichtbedingungen besser wachsen können da sie von den adulten Bäumen mit Kohlenhydraten versorgt werden. Unsere Resultate können diese Vermutung nicht stützen. Setzlinge beider Arten wachsen besser wenn sie nahe an adulten *Dryobalanops lanceolata* gepflanzt werden, dieser Effekt kann aber nicht auf das Ektomykorrhizen-Netzwerk zurückgeführt werden. Möglicherweise wachsen

*Dryobalanops lanceolata* Bäume an Standorten die für das Wachstum der Setzlinge optimaler sind, oder aber, dass Kohlenhydrate der adulten Bäum dieser Art im Boden in höherer Konzentration vorhanden sind und von den Setzlingen auch ohne Hyphen-Netzwerk absorbiert werden.

In der Generellen Diskussion am Schluss der Arbeit präsentieren wir für Kapitel 2 und 3 ein Gesamtkohlenstoff Budget, welches als Grundstein für zukünftige Messungen der Produktivität des Waldes dienen kann. Wir verstehen unter Produktivität ein Zuwachs der Biomasse, und somit des organisch gebundenen Kohlenstoffes über eine definierte Zeitspanne. Die Produktivität des Waldes konnte in dieser Studie nicht direkt quantifiziert werden, dies sollte aber Teil von zukünftiger Forschungsarbeit sein.

Für die Kapitel 4, 5 und 6 stellen wir die gewonnenen Erkenntnisse in Zusammenhang mit gängigen Theorien zur Koexistenz von Baum-Gilden in tropischen Regenwäldern. Wir verstehen eine Gilde hier als eine Gruppe von Arten der Flügelfruchtgewächse die ändernde Lichtbedingungen und Ektomykorrhizierung in ähnlicher Weise für das Wachstum nutzen. Wir beenden die Diskussion mit der Schlussfolgerung, dass die hier gezeigten Resultate dazu dienen, zu verstehen inwiefern potentiellen Nischenachsen – oder aber zufällige (neutrale) Prozesse – die Koexistenz von tropischen Bäumen der Flügelfruchtgewächse erklären können.

# 3 General Introduction

## 3.1 Scientific background

The most pressing question of the present century is how to make natural resources more productive to overcome humanities raising demands. The question is not necessarily about how to prevent climate change, nor is it necessarily about how to decrease a person's energy consumption or carbon footprint. The climate and its changes most likely cannot be effectively controlled and not even be predicted accurately in the near future. Once we consider future estimations of demography it is also unlikely that the current energy usage will cease (Field et al., 2004). In particular the demand for mobility, housing and farming–which take the largest share of our carbon footprint–are ascending due to increasing welfare around the globe. The impact of such development on natural ecosystems are manifold and irreversible. Humanity therefore needs in the first place innovations to increase the productivity of the natural resources that we use, only then are we capable to achieve much needed sustainable growth (Hoffert et al., 2002, Pacala and Socolow, 2004).

Forest is perceived as a natural resource that provides fundamental ecosystem processes which contribute to human well being (Chazdon, 2008). The loss of forest and associated ecosystem processes has implications on the global scale–such as climate regulation and a decrease in air quality or carbon sequestration; on a regional scale–such as lower water storage or increased soil erosion; and on a local scale–such as lower pest regulation, pollination, seed dispersal or soil generation and soil fertility (Guariguata and Balvanera, 2009). To date increasing demands for timber led to severe (>70 %) forest loss in half of the Asian nations (Laurance 2007). For Malaysia–where this study was undertaken–the extent of the remaining undisturbed forest cover was estimated at 11.6% (Billington 1996). Although little undisturbed forest remains, the situation is worse for degraded forest, as it is perceived as unproductive and therefore susceptible to conversion into oil palm (*Elaeis guinensis*) monocultures. The rate of forest loss of degraded forest in Malaysia increased from 0.3% per year during 1990-2000 to 0.8% between 2000-2005 (Koh, 2007).

In this thesis we perceive degraded forest as productive and show that it can maintain fundamental ecosystem processes. We define a forest as productive if tree biomass increases and subsequent removal of carbon dioxide ($CO_2$) from the atmosphere by sequestration of carbon in trees (Murray, 2009). Some argue that this is not the most critical ecosystem process in the short term–for example limited water access is more likely to directly impact human well being in the near future. However, there is a strong incentive to link carbon stored and exchanged in a forest with other fundamental ecosystem processes, such as water storage or the maintenance of high levels of biodiversity (Naidoo and Adamowicz, 2005). If a forest is valued and protected for its carbon stores this may directly affect water quality (Jackson et al., 2005) and provide shelter for all living associated (Bekessy and Wintle, 2008). It is therefore crucial to understand how a forest maintains different ecosystem processes and how these are interlinked (Simberloff, 1999). First experimental evidence for a multifunctional relationship between plant diversity and ecosystem processes was shown in grassland studies (Hector and Bagchi, 2007). Their results show that ecosystem multifunctionality depends on the number of species, because different species influence different ecosystem processes. Despite such experimental evidence the role of plant diversity for the maintenance of ecosystem processes in tropical forest communities is much debated on the basis of little experimental evidence (Kitayama, 2005, Wardle et al., 2005). Most recent studies on the relationship between tree diversity and productivity across natural forest and plantations were reported to be either positive (Erskine et al., 2006), negative (Firn et al., 2007) or hump-shaped (Potvin and Gotelli, 2008, Murphy et al., 2008, Healy et al., 2008). Such difference in response may be a result of differences in spatial scale, diversity levels or may change along the successional development of the forest (Vila et al., 2007). The Sabah Biodiversity Experiment, a forest rehabilitation project in North-East Malaysian Borneo, started in 2000 to test the plant diversity-productivity relationship for tropical mixed dipterocarp forest of South-East Asia. More than 100,000 seedlings of native Dipterocarpaceae trees were planted into randomly replicated 4 ha plots of

mono- and mixed cultures of 4- and 16-species. The Sabah Biodiversity Experiment forms part of a larger network of projects on forest restoration (Scherer-Lorenzen, 2007). Five forest diversity experiments with sites in Finland, Germany, China, Panama and Borneo were set up to test the relationship between productivity and fundamental ecosystem processes across continents and biomes, from boreal and temperate, to sub-tropical and tropical forest (Scherer-Lorenzen et al., 2005). A major obstacle of establishing such experiments is due to the fundamental biology of the study organism and their environment. For the Sabah Biodiversity Experiment three important constraints should be emphasized:

(i) The time frame for the experiment to be established is estimated at about 60 years, since dipterocarp trees grow at a rate of about 1 m $yr^{-1}$.

(ii) As these trees may grow up to 60 m, a respectable planting size for the experiment is at least 500 ha from a forest management perspective. This has direct implications on the establishment and maintenance effort, in particular with such a complex planting scheme.

(iii) In contrast to other forest diversity experiments, the Sabah Biodiversity Experiment was established in preexisting 30 year old logged forest with commonly applied rehabilitation techniques. The incentive was to test how standard practice may affect forest dynamics in the long term. The background vegetation and its effect on the planted trees therefore need to be assessed throughout the experiment.

Based on these premises the objective of the first three chapters is to advance our knowledge of the logged dipterocarp forest that the Sabah Biodiversity Experiment was established in. Our research questions are from a community ecology background with a special emphasis on logged forest stand diversity and associated carbon pools and fluxes. We lay the foundation for a quantitative survey of the organic carbon stored and exchanged in the logged forest of the study area. We recognize that an eventual study should relate productivity and ecosystem multifunctionality for the logged forest under study, however we could not test for this relationship at the current stage of the experiment. We also did not directly test

for the productivity of the logged forest as we present a mere starting point in a future series of measurements. In addition we present studies on the ecology of the Dipterocarpaceae by studying their response to changes of the environmental conditions in experiments set-up in shadehouse studies and the natural forest. The findings of this thesis may be of interest to persons interested in community ecology, conservation of biodiversity and restoration of tropical forests.

## 3.2 Thesis outline

In Chapter 1 we introduce the study site with a classification of the vegetation, the landscape, the geology and soil association. In addition we present rainfall data collected throughout the study phase at the local field station. This is the first descriptive study of the environmental conditions of the Sabah Biodiversity Experiment.

In Chapter 2 we estimate the six major carbon pools of the logged forest of the Sabah Biodiversity Experiment, namely above-ground tree biomass, above-ground nontree biomass, below-ground roots, forest floor litter, deadwood and soil organic carbon. We also present litterfall estimates taken over one year as an indicator for above-ground net primary productivity. Further, we show how estimated tree carbon stocks and tree diversity in logged forest differ from unlogged forest. These estimates serve as a baseline to predict how much carbon we expect to sequester by selectively planting trees, where we consider unlogged forest as the best case scenario.

In Chapter 3 we relate a major carbon flux–soil respiration–to forest composition and structure. We classify the forest stand of the Sabah Biodiversity Experiment into gap, pioneer, non-pioneer and mixed (pioneer, non-pioneer and unclassified trees) based on the tree species composition. Biotic factors, such as litterfall and fine root biomass, and abiotic factors, such as soil temperature and soil water content were measured to explain changes in day- and night time soil respiration rates of the different stands.

Chapter 2 and 3 are observational studies and a first attempt for a comprehensive baseline carbon and tree diversity estimation for the logged forest of the Sabah Biodiversity Experiment that can be used in future studies as a comparative measure of the experimental start.

Chapters 4, 5 and 6 focus on the ecology of selected dipterocarp species that we use as the planting stock for forest rehabilitation. In these chapters all findings are derived from experimental studies with a particular interest in plant growth under changing light environments (Chapter 4) and the influence of associated ectomycorrhiza on seedling growth performance (Chapter 5 and 6). Chapter 4 and 5 are from a shadehouse experiment set-up at the field station, whereas Chapter 6 is set-up in the logged forest of the Sabah Biodiversity Experiment.

In Chapter 4 we test for tree species coexistence mechanisms by experimentally forcing seedlings of six dipterocarp species into altered carbon balance by manipulating the light environment. We simulate gap dynamic processes (canopy gap opening and closure) to relate seedling growth to stored carbohydrate reserves. We test for a trade-off between carbohydrate allocation to either current growth or to stores for later survival after a gap opening. This is the first attempt to estimate dipterocarp growth with a semi-mechanistic model and to present size-corrected relative growth ($RGR_c$). In addition we present first evidence that Iditol—a sugar alcohol—may be a relevant component of carbohydrate reserves in dipterocarp seedlings.

In Chapter 5 we apply a soil sterilization treatment and subsequent inoculation with ectomycorrhiza and fertilizer to nursery raised seedlings of *Vatica albiramis* Van Slooten. We test if solarized soil (soil that was sterilized only by the heat of the sun), which is commonly used for planting seedling stock, leads to lower ectomycorrhizal association of the seedlings and subsequent growth decline. This is the first experimental study to control for the interactive effects of light, ectomycorrhiza and nutrient application on dipterocarp seedling growth.

In Chapter 6 we test for an ectomycorrhizal network between dipterocarp seedlings and adult trees of the same or differing species. Circumventing understorey seedlings from a potential connection to an ectomycorrhizal network should reveal if we find evidence of positive density dependent mechanisms for species coexistence. We expect that a seedling exposed to a sub-optimal light environment grows better than a competitor if it is associated to the ectomycorrhizal network and hence to the adult tree. This would indicate that adult dipterocarp trees in logged forest are not only an important seed source, but may also support the regeneration of their offspring and therefore cause a homogenous stand.

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# 4 Chapter One

## 4.1 Introduction to the Sabah Biodiversity Experiment

*(with R.C. Ong, manuscript)*

## 4.2 Lowland mixed dipterocarp forest

The world's forest cover almost 30% of the land surface and are divided into six categories: cool coniferous forest, temperate mixed forest, warm temperate moist forest, equatorial rainforest, tropical moist deciduous forest and dry forest (FAO, 2005). Tropical moist deciduous forest is found predominantly in America, Africa and South-East Asia, in areas with an average monthly temperature of 22-27 °C and an annual rainfall of 1250-2000 mm. Tropical forests of South-East Asia are estimated to be over 130 million years old and belong to the most complex and heterogenous ecosystems with over 2500 different species of trees and over 9000 species of flowering plants (Whitmore, 1998) (Fig.1). In the past the vegetation of Sabah covered a range of different forest types over an area of approximately 7.4 Mio ha, whereby mixed dipterocarp forest (80%), and in particular the lowland mixed dipterocarp forest were most widespread (47%) (Fig.2). Symington (1943) used the term lowland dipterocarp forest for primary climax forests of the plains, undulating land and foothills up to an elevation of about 300 m above sea level. It occupies the area from the inland limit of the Peat Swamp Forest to the lower limit of the Montane Forest. Lowland mixed dipterocarp forest is composed of several hundred tree species (Wyatt-Smith, 1995). The upper canopy is usually between 30 - 50 m high, although emergent trees commonly grow up to 60 m. About 50% of the upper canopy and the emergent trees is characterised by members of the Dipterocarpaceae (dipterocarp) family (genus Anisoptera, Dipterocarpus, Dryobalanops, Hopea, Shorea, Parashorea) (Wyatt-Smith, 1995). For example a *Shorea faguetiana* located in Tawau Hills Park, East Sabah, holds the record as the tallest tropical tree in the world with 88.33 m, ranking number 10 of the tallest trees in the world (Dial, 2007).

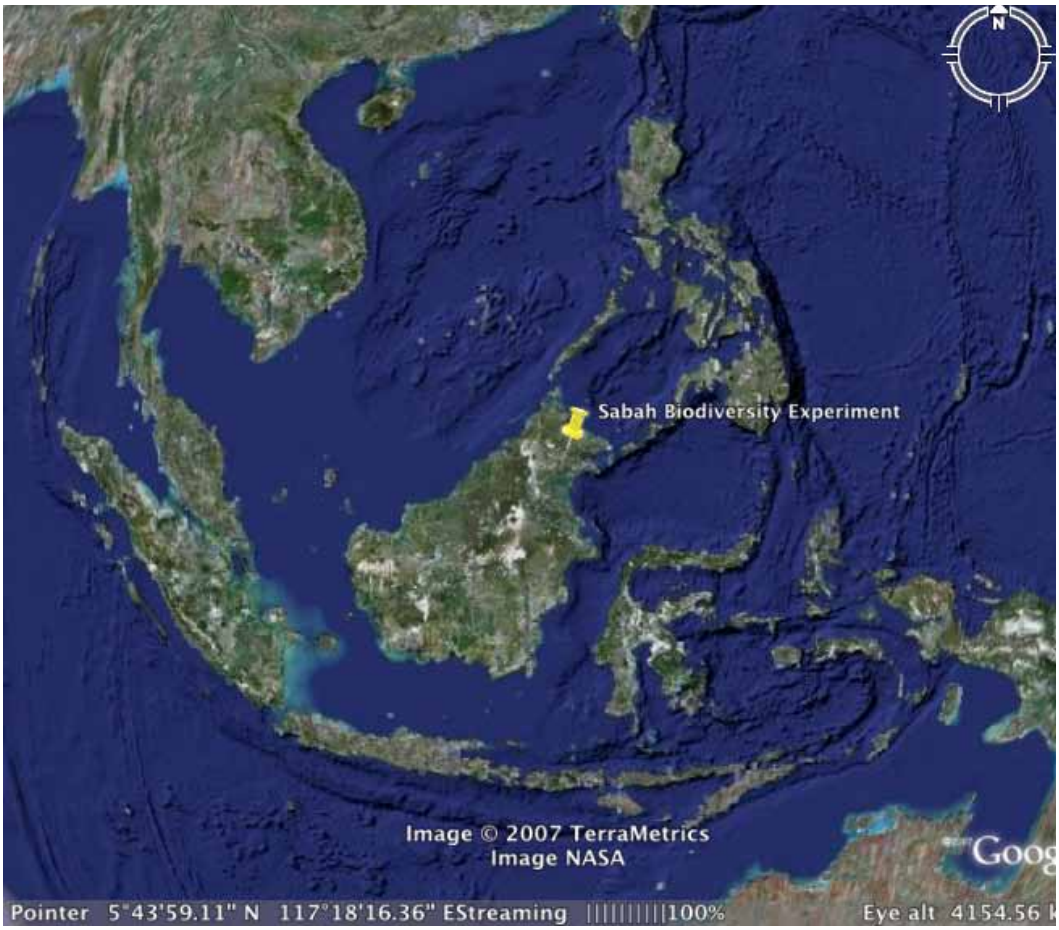


Figure 1 South-East Asia and the island of Borneo. The Sabah Biodiversity Experiment is situated in North-East Borneo.

## 4.3 Dipterocarp ecology

Forest Management has a long history in Malaysia (Appanah 2001) and is closely related to the ecology of the dipterocarps. Dipterocarps have intermittent mast fruiting events interspersed by irregular periods of low seed production (Ashton et al. 1988). This strategy may have evolved to satiate seed-predators and to ensure higher seed survival rates (Janzen 1974). It was suggested that such mastings are driven by El Niño induced droughts that trigger synchronous fruiting among dipterocarp tree species (Curran et al. 1999). However, forest degradation and subsequent loss have increased the frequency and intensity of droughts which may disorganise dipterocarp mastings and induce recruitment failure (Curran et al. 2004). According to some scientists no major fruiting events occured for the last ten years (C. Webb,

pers. comm). A consequence is that diverse seed sources are scarce in quantity and genetic variability. In addition dipterocarp seeds are recalcitrant, they germinate quickly after desiccation under moist and warm conditions (Appanah and Turnbull, 1998). Dipterocarps therefore form seedling banks instead of seed banks, whereby seedlings were shown to persist in understorey light conditions for years (Watling et al. 1997). The seedling bank should be a major concern during logging operation, because its destruction by heavy machinery and log extraction has a lasting effect on the subsequent regeneration of the logged forest which may take several decades (pers. observ.).

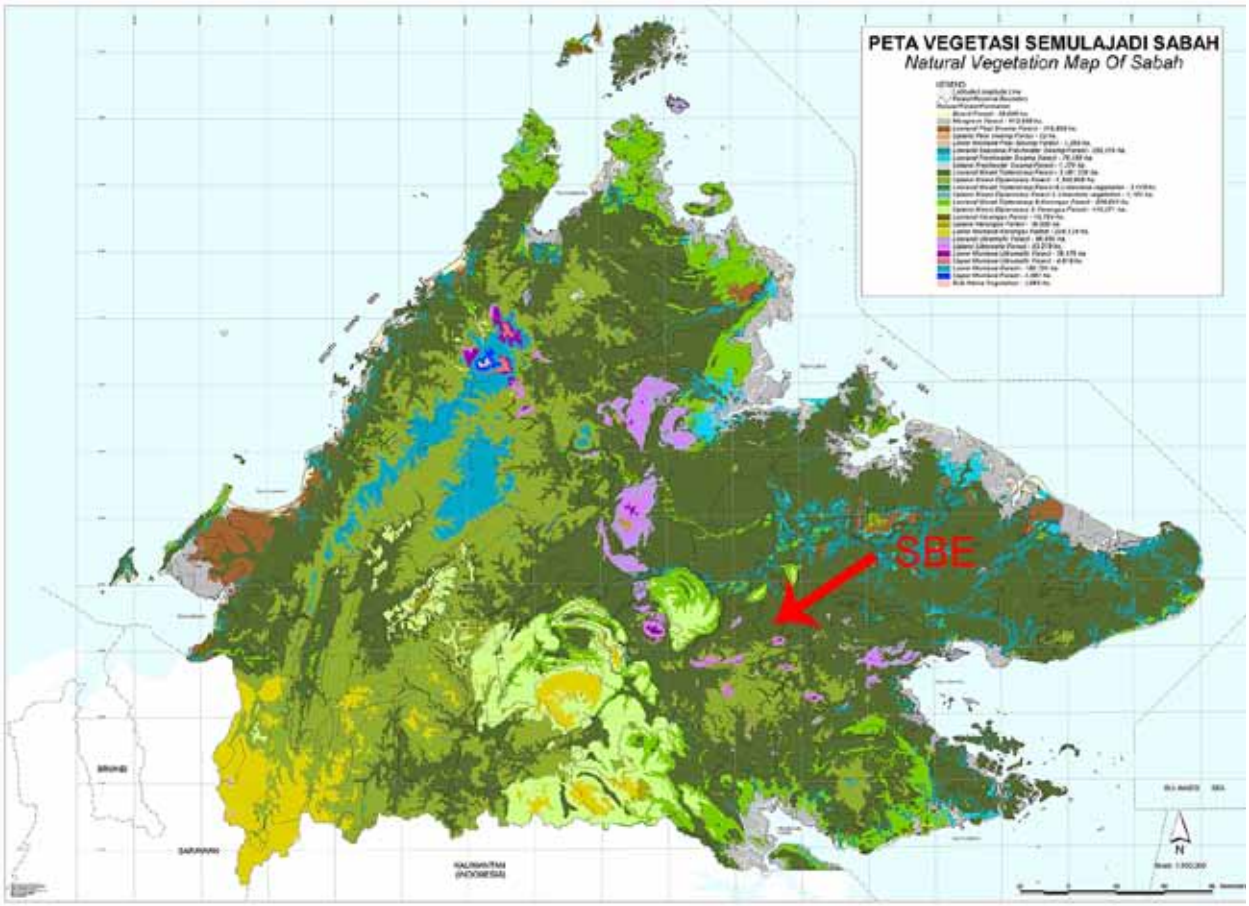


Figure 2 Vegetation map of Sabah (Source: Sabah Forestry Department), the location of the Sabah Biodiversity Experiment is indicated by the red arrow.

## 4.4 Timber extraction

Mixed dipterocarp forest comprises the bulk of commercially important timber in Malaysia (Ashton, 2008), whereby all forest lands are owned and managed by respective State Governments. Today about

50% of the original forest coverage of Sabah remains after four decades of commercial timber exploitation and subsequent conversion of the land into oil palm plantations (Bhagwat and Willis, 2008). Of the thousands of tree species about 100 are of economic importance, whereby approximately 70% belong to the Dipterocarpaceae. Timber is mainly exported to Japan, Taiwan, South Korea, Hong Kong, Singapore and India and is used for housing construction, as flooring material in freight containers, trucks and railcars and for dowels and mouldings (Sarawak Timber Industry Development Corporation, 2004). As a direct consequence, less than 15% of the original forest cover of Sabah is found to be in undisturbed condition whereby the remaining area is in degraded post-logging condition of various stages. The remaining forest of Sabah was divided into different forest reserve classes covering an area of 3.6 Mio ha, whereby commercial production forest (Class II) was allocated to 2.7 Mio ha (75%) thereof (Sabah Forestry Department, 2006). This forest is dedicated to logging to contribute to the State's economy and to increase the welfare of the local people of Sabah. The Innoprise Corporation Sdn. Bhd., a sub-branch of the Sabah Foundation (Yayasan Sabah) manages an area of about 1 Mio ha of Class II commercial production forest in the South-East of Sabah. The management of the remaining 1.7 Mio ha is unclear as no forest management plan exists to date, which is considered essential for sustainable forest management (Sabah Forestry Department, 2006) (Fig.3).

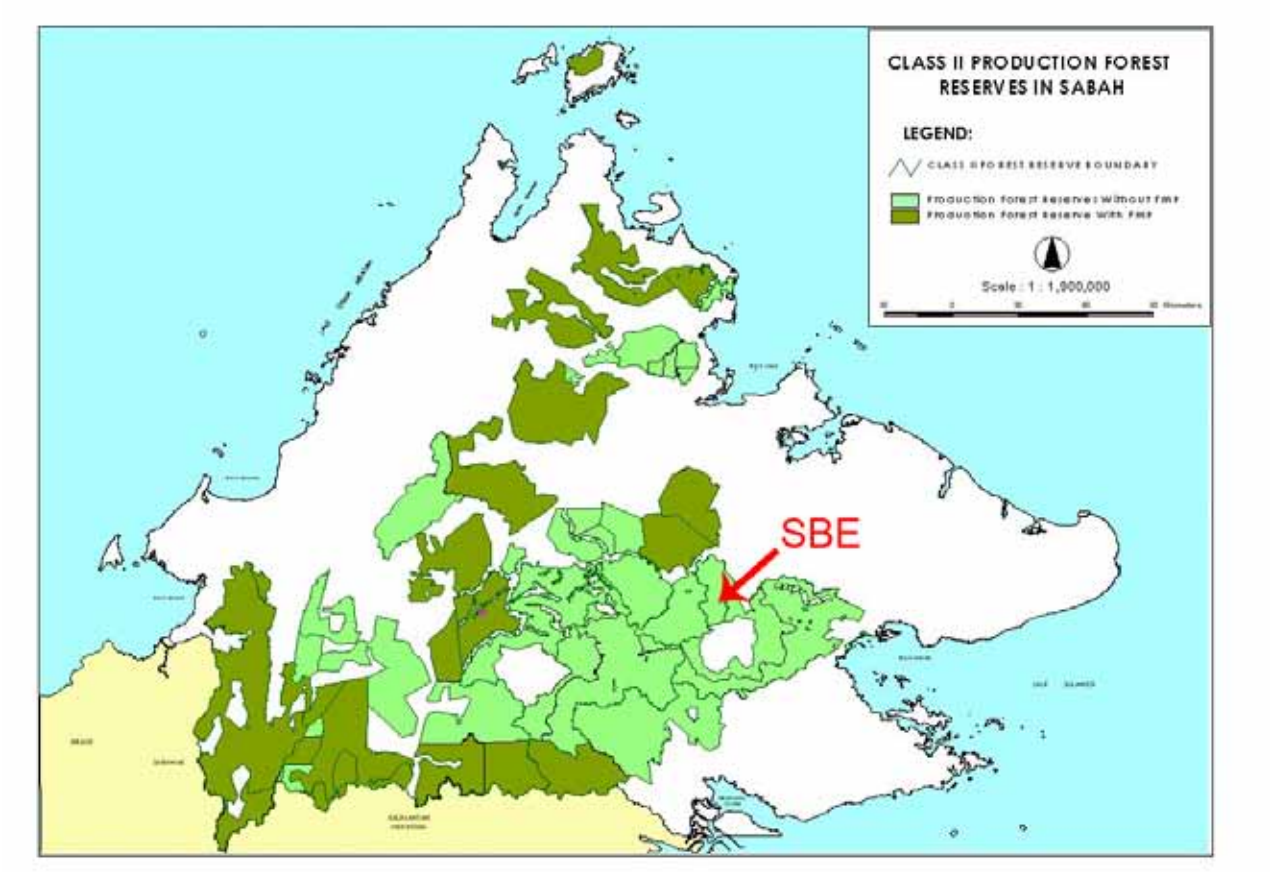


Figure 3 Designated Class II commercial production forest of Sabah (Source: Sabah Forestry Department). A forest management plan (FMP) is considered essential for sustainable forest management and exists for the light green but not for the dark green areas. The location of the Sabah Biodiversity Experiment is indicated by the red arrow.

## 4.5 Forest rehabilitation

Rehabilitation of previously logged forest is widely practiced in Sabah (Appanah and Khoo, 1996), in particular two treatments are applied in compliance with sustainable forest management. One is the selective liberation of potential crop trees by removal of overhead shade and cutting of vines and climbing bamboo. About 50,000 ha of logged-over production forest have been silviculturally treated with this method since 1997 (Sabah Forestry Department, 2006). The other treatment—enrichment planting—applies to poorly stocked logged forests. Here the number of native canopy trees in a previously logged forest is enhanced by selectively planting seedlings along lines or into gaps of the remaining forest (Adjers et al., 1995). Typically, 3 m planting lines are cut into the existing forest at 10 m intervals to allow planted seedlings to re-

generate at a density of 250 seedlings $ha^{-1}$ (Garcia and Falck, 2003). These cut lines are further maintained for approximately five years to ensure successful seedling establishment. Since the 1990's several large scale forest rehabilitation projects have been established, whereby they are all located within the concession area of the Sabah Foundation: the INIKEA project near Luasong, Kalabakan Forest Reserve (14,300 ha) (Garcia and Falck, 2003), the INFAPRO project in the Ulu Segama Forest Reserve (25,000 ha) (Nabuurs and Mohren, 1993) and the DERAMAKOT project in the Deramakot Forest Reserve (55,100 ha) (DIWPA, 2006, Martin et al., 2001). Further the Malua BioBank project in the Ulu Segama Malua Forest Reserve is currently established aiming at rehabilitating an area of 34,000 ha for long term biodiversity conservation (New Forests et al., 2008). In all projects members of the Dipterocarpaceae were predominantly used as the rehabilitation seedling stock due to their ecological and economic importance (Romell et al., 2008). Further, all projects at least to a certain extent (> 200 ha $yr^{-1}$ replanted), used the enrichment planting technique for measures of forest rehabilitation. In total about 20,000 ha of enrichment plantings have been carried out in production forests from 1992 to 2006 (Sabah Forestry Department, 2006). Along with these efforts to artifically regenerate previously logged forest the Sabah Biodiversity Experiment (500 ha), situated in the Malua Forest Reserve, was established to test for co-beneficial effects between planted tree diversity levels and ecosystem properties such as carbon retention on an experimental basis.

## 4.6 Malua Forest Reserve

The Malua Forest Reserve (34,000 ha) is located in the North-East of the Sabah Foundation Concession Area and borders the Danum Valley Conservation Area to the South. It was gazetted in 1961 and classified as Class II commercial production forest in 1984 (Sabah Forestry Departement, 2008b). The Malua Forest Reserve was logged during the early 1980s by Yeng Ho Hong Co. Ltd, a long term concessionaire. No detailed logging history was available at the time of writing, however reports from other logging coupes of

the Lahad Datu district indicate that yearly production volume was around 95–157 $m^3$ $ha^{-1}$ (1970-1980) and 75–134 $m^3$ $ha^{-1}$ (1980-1990) (unpubl. data, Danum Valley Field Centre). The forest quality of the area was assessed by visual interpretation of aerial photographs (1:17,500). The criterion for stratification is the number of trees ≥ 60 cm diameter at breast height, interpreted from crown size (SFD, 2005): Good forest (> 16 trees $ha^{-1}$), Moderate forest (9-16 trees $ha^{-1}$), Poor forest (5-8 trees $ha^{-1}$), Very poor forest (0-4 trees $ha^{-1}$), Shrubs/Grassland (none) (Fig.4). In 2006, the State Government approved sustainable forest management for the Ulu Segama (204,000 ha), Malua and Ulu Kalumpang (50,000 ha) Forest Reserves. In 2007, the Malua Forest Reserve was relogged and substantially degraded. A fifth of the logged area was designated to reduced impact logging measures, the remaining area was logged by conventional methods. The Ulu Segama-Malua area has a designated Forest Management Plan for 2008–2017 which describes the geology and the soils of the area (Fig.5) (Sabah Forestry Department, 2008).

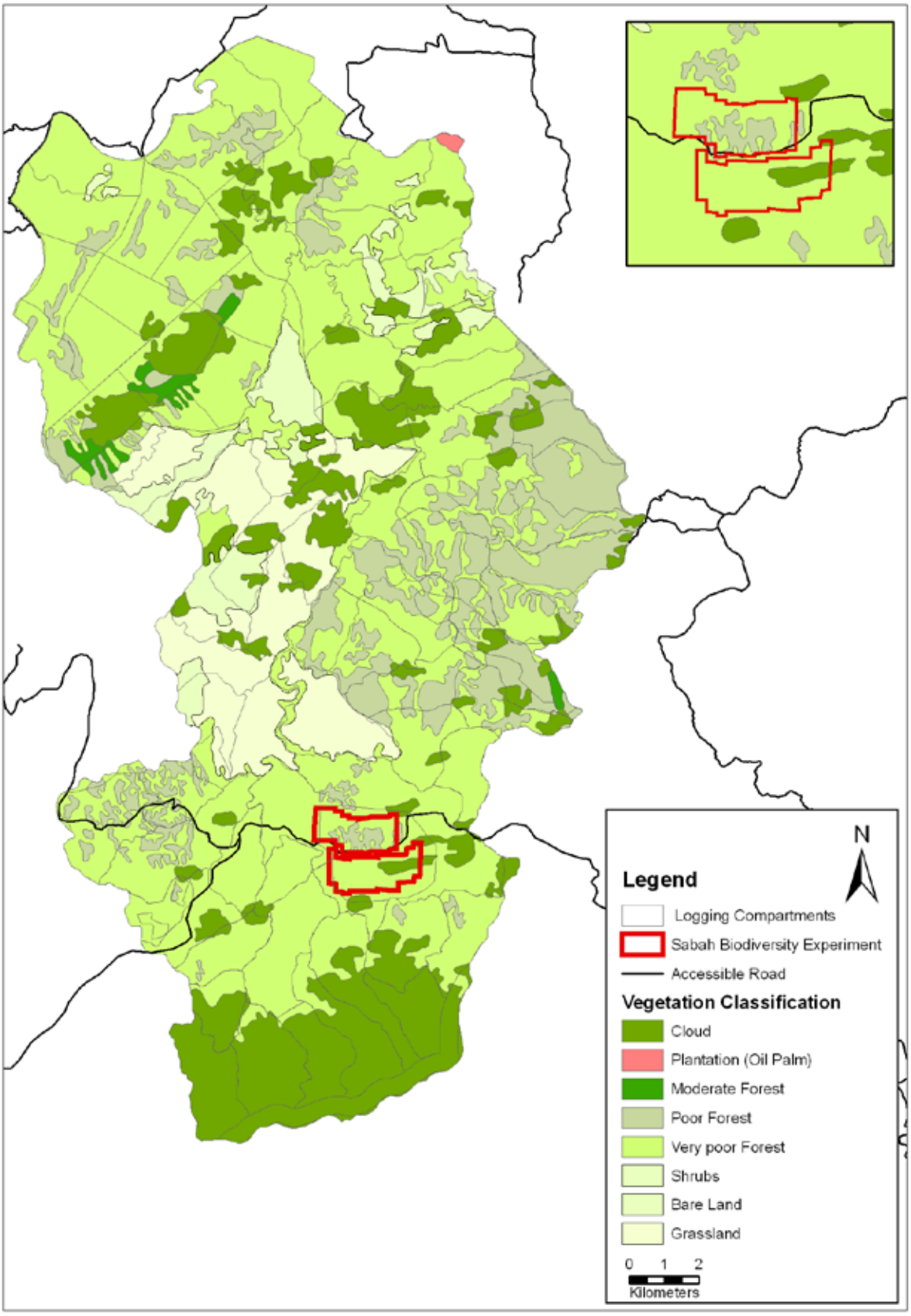


Figure 4 Vegetation classification of the Malua Forest Reserve and the Sabah Biodiversity Experiment (in red) (Source: Sabah Forestry Department).

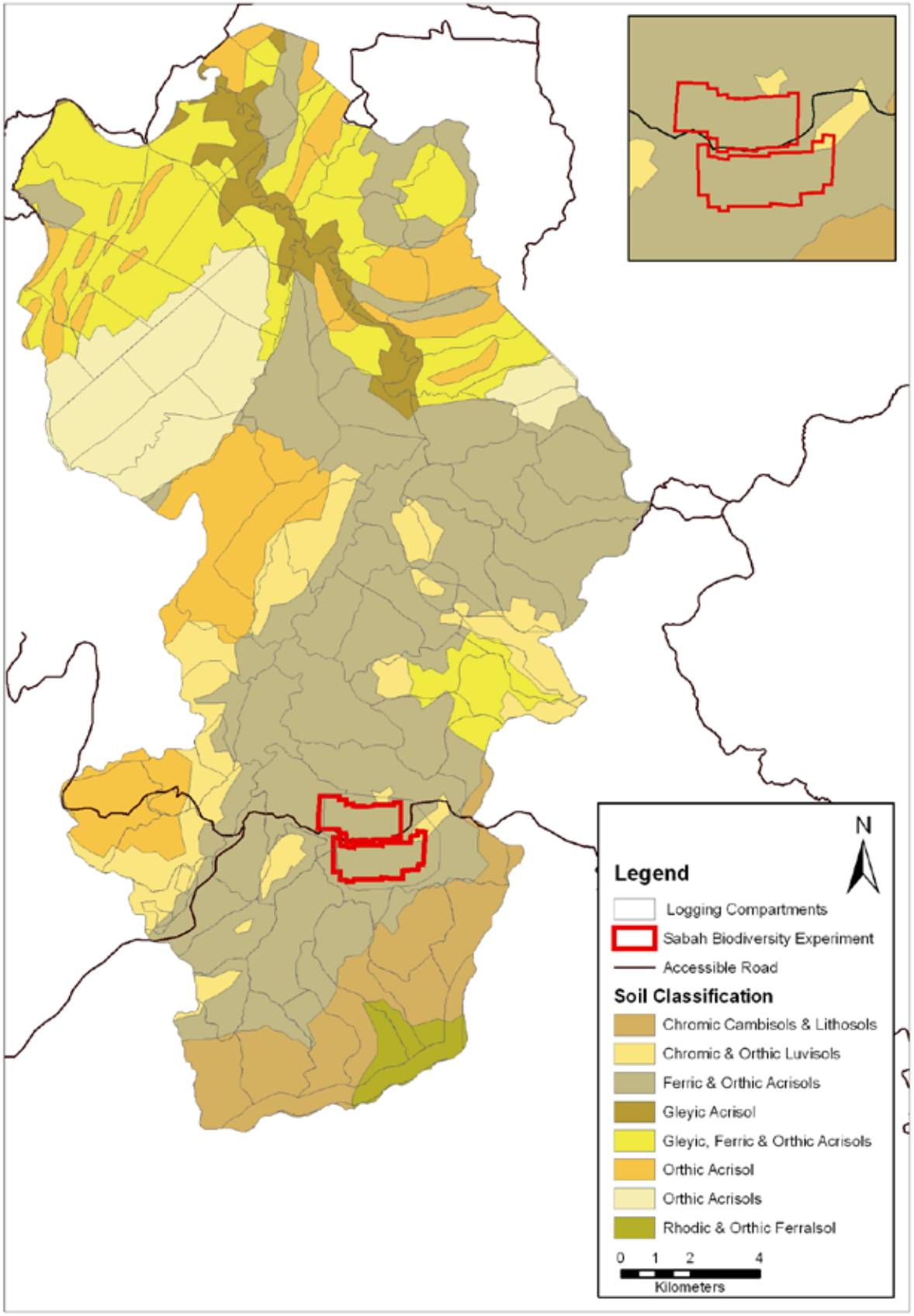


Figure 5 Soil classification of the Malua Forest Reserve and the Sabah Biodiversity Experiment (in red) (Source: Sabah Forestry Department).

## 4.7 The Sabah Biodiversity Experiment

The Sabah Biodiversity Experiment (N05°05'20" E117°38'32", 102 m.a.s.l.) is located in the southern part of the Malua Forest Reserve. By road, it is 65 km to the north of the Danum Valley Field Centre (Marsh and Greer, 1992). It was established in 2000 and therefore excluded from the most recent logging activity. Seedlings of native canopy tree species (Dipterocarpaceae) were planted in 124 4-hectare plots, in monocultures, four- and sixteen- species mixtures into the preexisting logged forest (Fig.6). The experiment aims to study the importance of a diverse tree community for providing fundamental ecoystem services, such as carbon sequestration (Scherer-Lorenzen et al., 2005). The long term carbon storage potential (>60 years) of the forest is expected to increase unequally, depending on the mixture of tree species planted. Out of the sixteen dipterocarp species planted as part of this experiment, five are listed as critically endangered (*Hopea ferruginea* Parijs., *Hopea sangal* Korth., *Parashorea malanonaan* (Blanco) Merr., *Shorea johorensis* Foxw., *Shorea macrophylla* Ashton) and four are listed as endangered (*Dryobalanops lanceolata* Burck, *Shorea argentifolia* Sym., *Shorea faguetiana* Heim., *Shorea leprosula* Miq.) according to the IUCN red list in 2008. The vegetation of the logged forest of the Sabah Biodiversity Experiment is classified as very poor forest with some cloud forest in the southern block (Block 1) and a mixture of poor to very poor forest in the northern block (Block 2) (Fig.4). An overview of the tree species diversity and carbon stocks of the Sabah Biodiversity Experiment is presented in Chapter 2.


Figure 6 Aerial view of the experimental set up of the Sabah Biodiversity Experiment (Source: Sabah Forestry Department). Each plot is 4 ha in size, seedlings were planted into the existing logged forest. The Malua Field Station is to the left of Plot 1 and close the Malua river.

### 4.7.1 Landscape, geology and soil classification

The area is located at the foothill of a ridge system along the south west boundary of the Malua Forest Reserve, with the most dominant elevation being Mount Nicola (917 m above sea level) (Marsh and Greer, 1992). The landscape is described as moderate hills with slopes between 0-20° and mountains. The soil belongs to the Kalabakan and the Mentapok association. The Kalabakan soil association forms in low hills and ridges with a relief amplitude of about 60 m and slopes between 10-20°. The soil is derived of mudstone and sandstone and consists of ferric and orthic acrisols (Sabah Forestry Departement, 2008a). Soils of the Mentapok association are derived from basic and intermediate igneous rocks of the basement complex and consist, amongst others of chromic and orthic luvisols (Marsh and Greer, 1992). They are formed in very steep hills with moderate to very steep slopes. Additional analysis indicated that the soil

is acidic (pH>5), highly weathered and low in available nutrient (81% base saturation). It has a marked increase of clay content with depth (Buringh, 1979) and a low organic carbon content (topsoil: 1.2 %, 1m depth: 0.6%).

### 4.7.2 Rainfall

In collaboration with the Sabah Meteorological Departement we established the first permanent meteorological station in logged forest of Sabah in 2008 to measure temperature, relative humidity, sun hours and cumulative rainfall on a daily basis. Cumulative daily rainfall is measured at 07:00 am using a standard rain gauge (Novalynx, USA). As part of this thesis we only present cumulative rainfall (mm) data during the course of the study (2005-2007) and relate it to readings of the Danum Valley Field Centre (unpubl. data) (Fig.7). Rainfall is expected to be higher during the Northeast monsoon from November to March and the Southwest monsoon during June and July (Marsh and Greer, 1992). The rainfall pattern was similar at both locations, with an exceptionally wet month in February 2006 and the driest months in March, April and May across all years. Interestingly the amount of cumulative rainfall was substantially higher in Malua across all years (24% in 2005 and 2006, 4% in 2007). We did not correct for potential differences in the methodologies of rainfall collection between the Malua Field Station and the Danum Valley Field Centre for the measurement period and can therefore not further comment the observed pattern. However, it would be interesting to relate the readings again in the future. We describe the forest as aseasonal with an expected annual rainfall of >3000 mm.

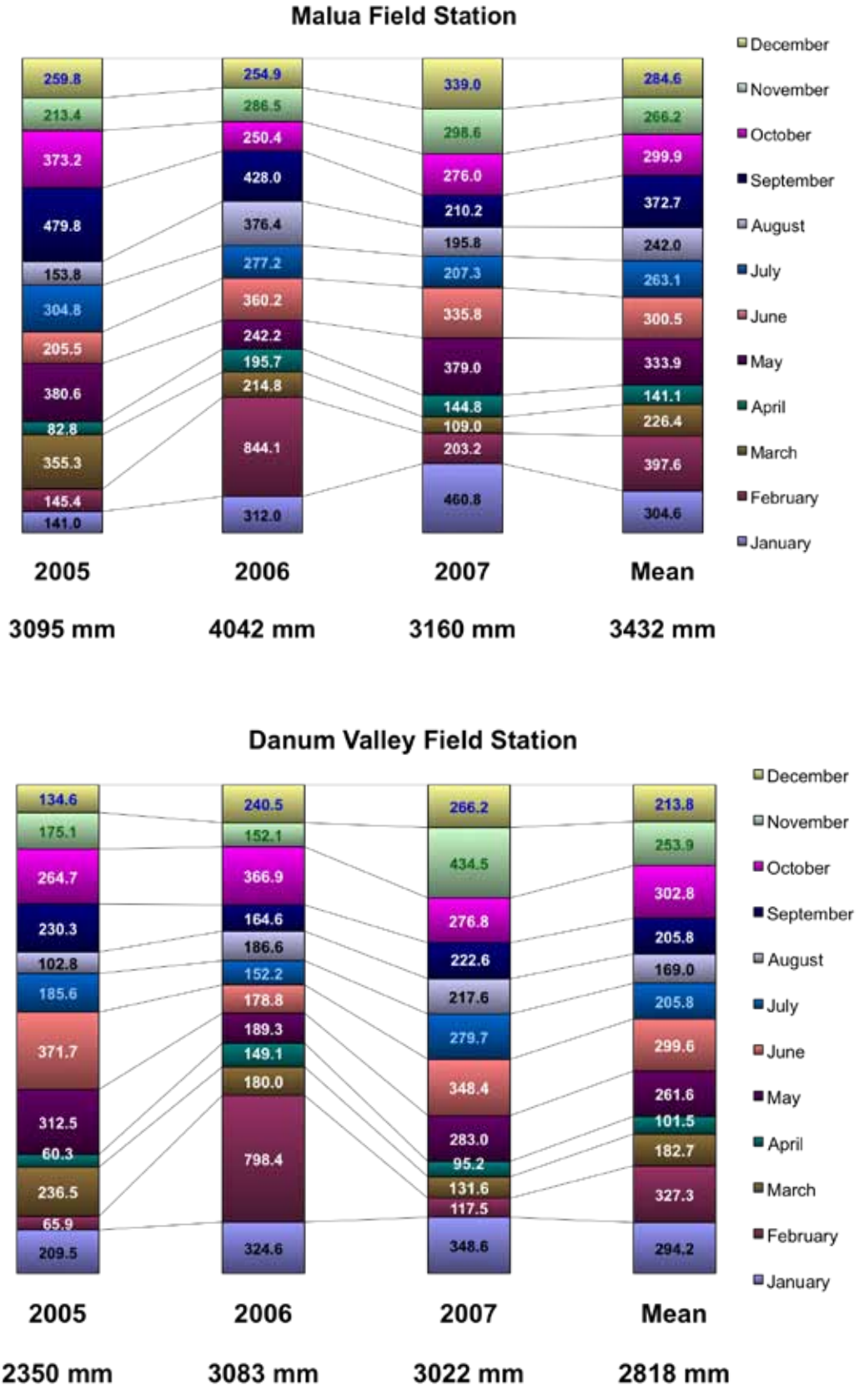


Figure 7 Monthly rainfall (mm) data for the study period at the study site (Malua Field Station) and at the Danum Valley Field Centre. Note the higher rainfall at Malua Field Station across all years.

## 4.8 Acknowledgements

We thank: Ronald Schmidt and Karin Beer for general help with ArcGIS; Abdul Malik Tussin and Edward Antonio Muthu from The Meteorological Department Sabah for setting up the Meteorological Station and training local field assistants at Malua in environmental data collection; The Sabah Forestry Department for providing information and maps of the Malua Forest Reserve.

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# 5 Chapter Two

## 5.1 Carbon Baseline Estimation of the Sabah Biodiversity Experiment

*(with Y.Y. Lee, R.C. Ong, A. Hector, manuscript)*

## 5.2 Abstract

The Sabah Biodiversity Experiment is a 500 ha forest rehabilitation project that started in the year 2000 in North Borneo. We present a full baseline carbon estimation for the existing logged forest of this area. In total all six major carbon pools contributed to 237.2 Mg C $ha^{-1}$ ± 8.4 (SD): Above-ground tree biomass (57%), above-ground non-tree biomass (2%), below-ground roots (10%), forest floor litter (<1%), deadwood (6%), and soil (25%). In addition we compared the above-ground tree biomass–the largest contributor to total organic carbon stocks–and tree diversity of the logged forest (Sabah Biodiversity Experiment) to unlogged forest (Danum Valley). Above-ground tree biomass was marginally lower (Mean difference -196.5 Mg $ha^{-1}$; with 95% CI = -408.7 to 15.6) in the 30 year old logged forest study area than in unlogged forest. We argue that logging decreased tree biomass which could not be regained over 30 years as pioneer trees–with typically lower wood density–occupied the area that was previously dominated by large dipterocarp trees. Tree α diversity was found to be significantly higher in logged forest compared to unlogged forest, which may be an effect of the small scale (1 ha) sampling of the study. Indicator species of forest disturbance (*Macaranga pearsonii* and *Macaranga gigantea*) suggest that the area should be classified as heavily disturbed secondary forest. In contrast, indicators of nutrient and carbon turnover rates, in particular dead standing wood, fine roots and litterfall, were not found to be significantly different compared to unlogged forest. This suggests that a 30 year old logged forest can fully maintain these ecosystem processes and its conservation value should therefore be reassessed. Here we provide ground measurements for 30 year old logged forest that can be incorporated into more extensive studies. We conclude that more extensive work on the relationship between carbon storage, carbon turnover rates and tree diversity is needed for North Borneo.

**Keywords**

carbon cycle, Borneo, tree diversity, logged forest

## 5.3 Introduction

Forest ecosystems contain an estimated 638 gigatonnes (60%) of the carbon stored in terrestrial ecosystems and could potentially absorb about 10% of global carbon emissions projected for the first half of this century (Streck et al., 2008). At the same time 13 million hectares of tropical deforestation per year contribute to 20% of global carbon emissions (Canadell et al., 2008). The increasing importance of the remaining tropical forests for climate change mitigation is therefore a topic of broad interest (Field et al., 2004, Chazdon, 2008, Keith et al., 2009). Forest cover of the Indo-Malaya region (including South Asia, Southeast Asia, and Papua New Guinea) was less than 40 % of the original area by 2000 (Wright and Muller-Landau, 2006). For the island of Borneo forest cover (of all types combined) was estimated at 57% in 2002 with an annual deforestation rate of 1.7% (Langner et al., 2007). Intense logging in Sabah peaked between 1980 and 1990, when primary forests were exploited as part of the tiger economy of Malaysia and still make up a major part of Sabah's economy (Langner et al., 2007, Bennett et al., 2000). Rehabilitation of previously logged forest is widely practiced in Sabah (Appanah and Khoo, 1996). Since the 1990's several large scale forest rehabilitation projects have been established, namely the INIKEA project near Luasong (14,300 ha) (Garcia and Falck, 2003), the INFAPRO project in the Ulu Segama Forest Reserve (25,000 ha) (Nabuurs and Mohren, 1993) and the DERAMAKOT project in the Deramakot Forest Reserve (55,100 ha) (Martin et al., 2001, DIWPA, 2006). Further the Malua BioBank project in the Ulu Segama Malua Forest Reserve is currently being established aiming at rehabilitating an area of 34,000 ha for long term biodiversity conservation (New Forests et al., 2008). Along with these efforts to artificially regenerate previously logged forest the Sabah Biodiversity Experiment (500 ha), situated in the Malua Forest Reserve, was established to test for co-beneficial effects between planted tree diversity levels and ecosystem properties such as carbon retention on an experimental basis (Scherer-Lorenzen et al., 2005).

All these projects are part of an one million hectare concession area which belongs to the publicly owned Sabah Foundation. Its purpose is to increase the welfare of the local people of Sabah, by exploiting common natural resources such as timber (Marsh and Greer, 1992). In all projects members of the Dipterocarpaceae were predominantly used as the rehabilitation seedling stock due to their ecological and economic importance (Romell et al., 2008). Further, all projects at least to a certain extent (>200 ha $yr^{-1}$ replanted), used the enrichment planting technique for measures of forest rehabilitation. Whereby the number of native canopy trees in a previously logged forest is enhanced by selectively planting seedlings along lines or into gaps of the remaining forest (Adjers et al., 1995). Typically, 3 m planting lines were cut into the existing forest at 10 m intervals to allow planted seedlings to regenerate at a density of 250 seedlings $ha^{-1}$ (Garcia and Falck, 2003). These cut lines were further maintained for approximately five years to ensure successful seedling establishment.

An essential part of such a restoration effort is to measure changes that can be accounted to the silvicultural treatment. Any changes that occur as part of natural forest regeneration should be subtracted (Moura-Costa et al., 1996). To determine the carbon offset potential of forest rehabilitation it is crucial to establish the carbon baseline, monitor changes in carbon stocks, monitor leakage (increased emissions as a direct cause of the project) and estimate project emissions (Streck et al., 2008). The long term objective of the Sabah Biodiversity Experiment is to assess influences of tree diversity on associated ecosystem processes such as carbon storage. Hence it is crucial to determine both, the tree diversity and carbon stocks of the natural forest at the baseline. Tree biomass is known to constitute the majority of the carbon stock changes in any land-based project (Streck et al., 2008) and is the main focus of this study. Our intention was to compare both, above-ground tree biomass and tree diversity of the Sabah Biodiversity Experiment to undisturbed close-by forest of the Danum Valley Conservation area (43,800 ha) (Marsh and Greer,

1992). Such a comparison would reveal to what extent 30 year old logged mixed dipterocarp forest could regenerate from human-induced disturbance.

In addition we provide a carbon baseline estimation for the 30 year old logged forest covering the area of the Sabah Biodiversity Experiment. We report estimates for all six carbon pools; Above-ground tree biomass, above-ground non-tree biomass, below-ground roots, forest floor litter, deadwood, and soil. In addition we present litterfall rates taken over one year for the logged forest under study (Proctor, 1984, Yamashita et al., 1995). Aside from above-ground tree biomass all other carbon pools were measured in logged forest only and were compared to published studies from unlogged forest. Our estimations are based on crude methods and do not use the best current knowledge to measure each individual pool (see Litton et al. (2007) for a method discussion). The estimates should be interpreted with care and only provide a general guideline to identify the most important carbon pools. Nevertheless, such information is much needed, since compared to current research activities on the topic in the Amazon (see Malhi et al. (2009) for a recent review) there is substantial lack of information for tropical forests of South-East Asia. Despite the fact that Borneo is regarded as a biomass hotspot in tropical forests of Asia (Lasco and Pulhin, 2004) estimates of biomass and carbon stocks are still scarce. For example the last global forest resource assessment of carbon stocks in Malaysia (FAO, 2005) was based on estimates from Peninsular Malaysia only, due to the lack of appropriate data from the provinces of Sabah and Sarawak. Here we provide such data for 30 year old logged mixed dipterocarp forest.

## 5.4 Material and Methods

### 5.4.1 The Malua Forest Reserve

The Malua Forest Reserve is located in the eastern part of the province of Sabah in Malaysian North Borneo. It borders the Danum Valley Conservation Area to the South and consists of approximately 35,000 ha of secondary lowland dipterocarp rainforest, the most widespread forest type in equatorial South East Asia (Marsh and Greer, 1992). The forest is aseasonal with an expected annual rainfall of >3000 mm (Chapter 1). The Malua Forest Reserve was logged during the early 1980s by Yeng Ho Hong Co. Ltd, a long term concessionaire. No detailed logging history was available at the time of writing, however reports from other logging coupes of the Lahad Datu district suggest that yearly production volume was around 95–157 $m^3$ $ha^{-1}$ (1970-1980) and 75–134 $m^3$ $ha^{-1}$ (1980-1990) (Danum Valley Field Centre). In 2007, the Malua Forest Reserve was relogged and substantially degraded (pers. observ.). A fifth of the logged area was designated to reduced impact logging measures, the remaining area was logged by conventional methods.

### 5.4.2 The Sabah Biodiversity Experiment

The Sabah Biodiversity Experiment (N05°05'20" E117°38'32", 102 m.a.s.l.) is located in the southern part of the Malua Forest Reserve. By road, it is 65 km to the north of the Danum Valley Field Station. It covers an area of approximately 500 ha of logged forest and was established in 2000 and therefore was excluded from the most recent logging activity. Seedlings of native canopy tree species (Dipterocarpaceae) were planted in 124 4-hectare square plots (200 x 200 m), in monocultures, four- and sixteen- species mixtures into the preexisting logged forest. The experiment aims to study the importance of a diverse tree community for providing fundamental ecosystem services, such as carbon sequestration (Scherer-Lorenzen et al., 2005). The long term carbon storage potential (>60 years) of the forest is expected to

increase differently, depending on the mixture of tree species planted. Out of the sixteen dipterocarp species planted as part of this experiment, five are listed as critically endangered (*Hopea ferruginea* Parijs., *Hopea sangal* Korth., *Parashorea malanonaan* (Blanco) Merr., *Shorea johorensis* Foxw., *Shorea macrophylla* Ashton) and four are listed as endangered (*Dryobalanops lanceolata* Burck, *Shorea argentifolia* Sym., *Shorea faguetiana* Heim., *Shorea leprosula* Miq.) according to the IUCN red list in 2008.

The soil of the experimental area was classified as orthic acrisol, which is acid (pH>5), highly weathered and low in available nutrient (81 % base saturation). It has a marked increase of clay content with depth (Buringh, 1979) and a low organic carbon content (topsoil: 1.2%, 1m depth: 0.6%). Bedrock consists of a mixture of mudstone and sandstone areas with miscellaneous rocks (Sabah Forestry Department, unpubl. data).

### 5.4.3 Tree inventory

The tree inventory was taken in the background logged forest of the Sabah Biodiversity Experiment (no enrichment planted trees in inventory) and in unlogged forest close to the Danum Valley Field Station. At both sites four 250 meter long transect lines, each 100 meter apart, were orientated along a North-South axis to describe the stand structure of the forest in July 2008. Lines and orientation were measured with a handheld GPS to 10 m accuracy (GPSMAP 60 CSx, Garmin, USA). All trees >10 cm diameter breast height (DBH) that were within five meters on each side of the transect line were tagged, measured with a DBH tape (Yamayo, Japan) and identified to species or, if unknown, to genus level (Table S2). We followed the RAINFOR field manual of Philips and Baker (2002) to measure all trees in a comparable standard way. If a tree showed large buttresses its DBH was measured just above the buttresses using a ladder. It was suggested that DBH measures above buttresses may substantially underestimate basal area of large trees by ignoring the area occupied by the buttress base (Clark and Clark, 2000). However, for

logistic reasons we did not calculate basal area of the buttress for every individual large tree and measured DBH above the buttress only. In total we measured 410 individual trees (>10 cm DBH) in the unlogged forest and 417 trees in the logged forest.

### 5.4.4 Tree diversity

We present estimates of numbers of individual tree species as Fisher's α (Fisher et al., 1943) and Whittaker's diversity (Whittaker, 1960), where α diversity is for a given transect and β diversity is the difference between replicate transects within a given forest type (i.e. logged forest versus unlogged forest). Alpha (α) diversity can be interpreted as the small scale diversity within replicate transects, it describes the number of rare species represented by only a single individual (Whittaker, 1972):

$$S = \alpha \ln(1 + N / \alpha) \quad (1)$$

where S is the total number of species and N is the number of individuals. Confidence limits were set by:

$$\text{var}(\alpha) = \frac{0.693147\ \alpha}{\left[\ln(x / (1 - x) - 1\right]^2} \quad (2)$$

where x (0<x<1) is a constant that is estimated from an iterative solution (Magurran, 2004). Beta (β) diversity can be interpreted as a measure of between-forest type diversity, it describes how much the diversity of two or more spatial units differ (Whittaker, 1972):

$$\beta = S / \bar{\alpha} \quad (3)$$

where S is the total number of species and α is the average sample diversity, whereby each sample is a standard size and diversity is measured as species richness (Magurran, 2004).

### 5.4.5 Above-ground tree biomass

Tree biomass calculations were based on stem height and volume equations (Forestal International Limited, 1973). The equations were developed with destructive sampling of trees in the Ulu Segama Forest Reserve, which is adjacent to the area under study. The general equation form for height was a quadratic polynomial of the form: $H = a + bD+cD^2$, where H is height, D is DBH and a, b, c are tree group specific parameters (Table S1). Volume equations were derived for fifteen species groups using the general form $V = a + b(D^2H/100)^2 + c((D^2H)/100)^2$ where V is volume. We used the equations of Pinard (1995) to calculate volume estimation per individual tree, which were adapted from data collected by Forestal International Limited (1973) (Table S1). Volume was multiplied with wood density estimates and a biomass expansion factor of 1.9 for logged tropical secondary forest (Brown et al., 1989). The biomass expansion factor is defined as the ratio of total above-ground biomass to commercial stem biomass. To receive a conservative estimate for the difference in tree biomass between logged and unlogged forest we calculated both with the same expansion factor. Individual tree biomass (Mg) was summed for each transect line (n = 4). There may be considerable source of error in these estimations that may bias the estimates of carbon stocks in trees. In particular the quality of the model, the size of the sampled area, the representativity of the plots and an appropriate wood density should be considered (Baker et al., 2004, Chave et al., 2004). In our case the quality of the allometric estimates may have led to the largest error propagation, in particular since we applied it to both, logged and unlogged forest. Several published allometric models were considered for direct comparison (Kato et al., 1978, Brown, 1997, Ketterings et al., 2001, Chave et al., 2005, Basuki et al., 2009) whereby all estimated larger above-ground tree biomass (357-517 Mg $ha^{-1}$) compared to the method we used. Only the proposed model of Banaticla et al. (2005) from tree plantations of the Philippines was similar (273 Mg $ha^{-1}$) to the estimations with allometric equations of Forestal International, adapted by Pinard (1995). The next closest model (357 Mg $ha^{-1}$) was the one proposed

by Ketterings et al. (2001) from secondary forest of Sumatra, Indonesia. Site specificity is known to be of importance for the selection of allometric models (Chave et al., 2004, Basuki et al., 2009), therefore we chose the most conservative approach by taking the geographically closest model derived, which also led to lowest estimations for aboveground tree biomass. The size of the sampled area was one hectare (4 transect lines, each 250 x 10 m) for unlogged and logged forest. Sample area size was shown to be crucial for estimating levels of tree diversity (Ashton 2008), however limited resources did not allow for a more exhaustive survey. Our findings were in line with previous reports of the same study area regarding both, tree diversity (Berry et al., 2008, Bischoff et al., 2005) and carbon stock estimations (Pinard and Putz, 1996). The sampled plots in unlogged forest were close to the Danum Valley Field Station (W6 to W9), near to previously published studies (Burghouts et al., 1992, Newbery et al., 1992, Bischoff et al., 2005, Berry et al., 2008). For logged forest transect lines were selected in the North Block (Plot 65-124) of the Sabah Biodiversity Experiment. The forest in this area is dominated by pioneers and more degraded than other areas because it is relatively flat with moderate hills (slope 0-20 degrees) (Chapter 1).

### 5.4.6 Wood density

Wood density values were taken from the World Agroforestry Centre (WAF) Wood Density Database to convert volume estimation into individual tree biomass. We defined wood density as the oven-dry weight of wood divided by its wet volume (Fearnside, 1997). Wood cores (n = 2 per species) of eighteen local tree species (including the nine most common ones) were taken with an increment borer at 1.3 m height (Haglöf, Sweden). Wood density values were calculated using the water-displacement method described in Chave (2005). Cross reference with the WAF wood density database shows that the correlation between our site and their proposed wood densities is a good approximate across species (Fig.8). If the species was unknown or the wood density not available we took mean wood density of the genus as a substitute

(Chave 2005). In the few cases (<4 cases) where genus wood density was not available we took the mean overall wood density (610 kg $m^{-3}$) as a substitute.

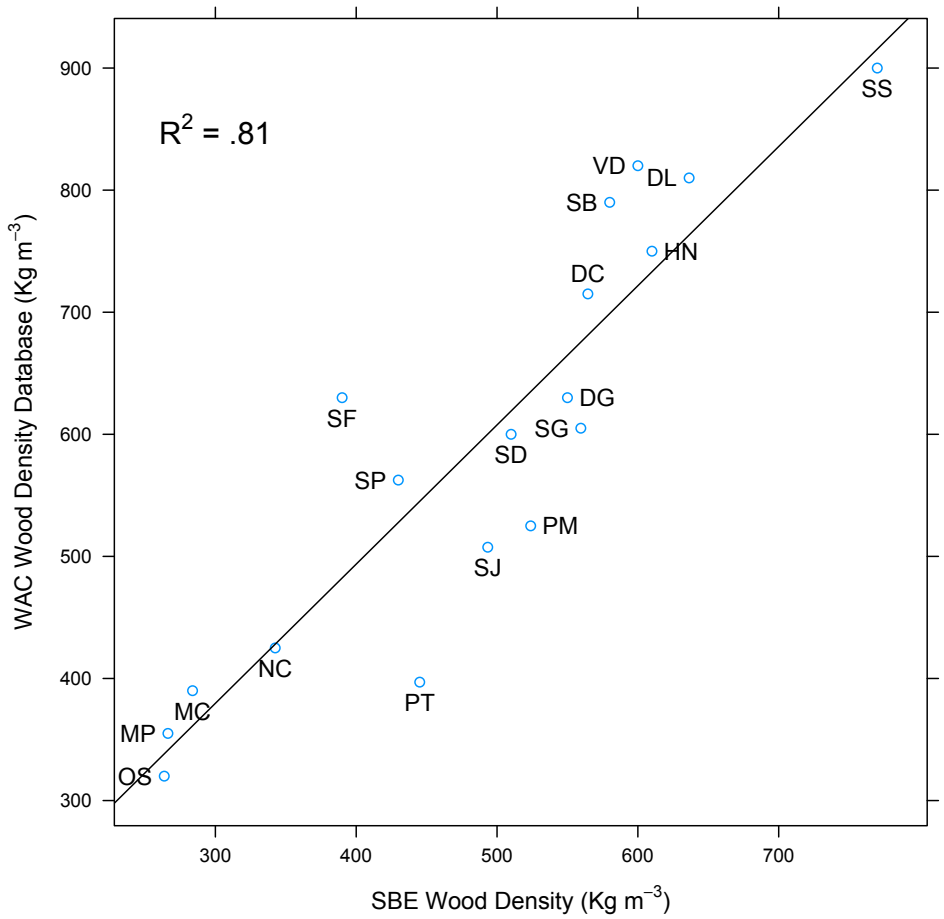


Figure 8 Wood density comparison between the World Agroforestry Centre (WAC) Wood Density Database and own collected Wood Density measures from the Sabah Biodiversity Experiment (SBE). Species in bold belong to the ten most important species in terms of basal area. DC: *Dipterocarpus caudiferus*, DL: *Dryobalanops lanceolata*, DG: *Durio grandiflorus*, HN: *Hopea nervosa*, MG: *Macaranga gigantea*, MP: *Macaranga pearsonii*, NC: *Neolamarkia cadamba*, OS: *Octomeles sumatrana*, PM: *Parashorea malaanonan*, PT: *Parashorea tomentella*, SD: *Saraca declinata*, SF: *Shorea fallax*, SG: *Shorea gibbosa*, SJ: *Shorea johorensis*, SP: *Shorea parvifolia*, SS: *Shorea superba*, VD: *Vatica dulitensis*.

### 5.4.7 Above-ground non-tree biomass

Six quadrats (5 x 5 m) along each transect line in the logged forest were randomly selected (n = 24) in October 2007. Within the quadrat we measured the basal diameter (10 cm above ground) and DBH of all saplings (< 10 cm DBH and > 2 m height), seedlings (< 2 m height), lianas and woody vines. Diameter was estimated from two measurements taken perpendicular to each other with a standard caliper. Lianas

were measured 1.3 m along the stem from the point where they entered the ground. Saplings, seedlings and all woody vines within each quadrat were harvested. All saplings were individually measured using a common spring scale. Wet biomass for seedlings was measured once for all seedlings together. A subsample of saplings and seedlings was dried to constant mass (7 days, 60°C) to relate wet to dry biomass ($y = 0.55x$, $R^2 = 0.98$, $n = 76$, intercept was set to zero). One *Eusideroxylon zwagerii* (belian) sapling was not harvested due to its age and size (probably about 30 years, 5.2 cm DBH).

### 5.4.8 Standing litter and fine roots

We established 0.5 x 0.5 m subquadrats within each quadrat to collect all woody debris and leaf litter separately. In each subquadrat we also took vertical soil cores (100 $cm^3$) at the soil surface (0-5 cm) using standard soil corers (Eijkelkamp, Netherlands). Fine roots (≤2 mm diameter) were extracted by washing the soil cores over a 210 µm sieve (Retsch, Germany). All collected samples were dried in a glasshouse (7 days, 60°C) before measuring their dry biomass with a precision scale. Coarse root biomass (>2 mm diameter) estimation was based on measurements from Pinard (1997), where they reported coarse roots to be 17% of AGB.

### 5.4.9 Litterfall

Litterfall traps (1 $m^2$) were randomly allocated along the transect lines in the logged forest at 1.3 m height, using fine meshed plastic net ($n = 40$). Litter was collected every other week over one year (June 2006 – June 2007, $n = 25$). Litter was further separated into leaves, twigs (typically < 1 cm in diameter) and reproductive organs (flowers and fruits) (Yamashita et al., 1995). Litterfall samples were dried in a glasshouse (7 days, 60°C) before measuring their biomass with a precision scale.

### 5.4.10 Deadwood

DBH, height, degradation state (not degraded, degraded, heavily degraded) and tree structure (stem only/ stem plus branches) was noted for all dead standing trees in the logged forest that were within five meter on each side of the transect lines. We estimated the height of standing trees and calculated tree volume of dead standing trees following the method of Gale (2000). Due to the lack of correct wood density estimates for sampled dead trees we assumed a wood density of 500 kg $m^{-3}$ for dead standing trees as reported from Venezuela (Delaney et al., 1998).

### 5.4.11 Soil organic carbon

Soil core samples were taken from the middle of the thirteen unplanted 4 ha control plots in the logged forest of the Sabah Biodiversity Experiment in June 2006. The plots were randomly allocated throughout the 500 ha area and should therefore represent large scale spatial variability. At each plot we excavated three 1 m soil pits, each located 10 m away from the middle of the plot directed either South, Northwest or Northeast. Soil cores (100 $cm^3$) were inserted horizontally down to one meter depth at different layers (0–5, 5–10, 10–20, 20–30, 30–40, 40–50, 50–60, 60–70, 70–80, 80–90, 90–100 cm) using standard soil corers (Eijkelkamp, Netherlands) and a rubber hammer (n = 396). The three replications (South, Northwest and Northeast) of each layer in each plot were pooled for subsequent soil analysis to include site variability. Damp soil samples were laid out to dry in trays in a well ventilated room until the soil sample weight became quite consistent (about 5 days to a week depending on the initial conditions of the samples). Rock and root components were separated from each sample. Weight and volume was determined using the water (rock) and ethanol (roots) replacement method. Bulk density was derived with the equation:

$$BD = {MS - MR}/{VS - VR} \qquad (4)$$

where BD is bulk density (g $cm^{-3}$), MS is mass of the dry soil (g), MR is mass of rocks and roots (g), VS is volume of dry soil (ml) and VR is volume of rocks and roots (ml). Samples were further ground with a porcelain mortar and pestle to pass through a 2 mm sieve (Majalap and Chu, 1992).

### 5.4.12 Carbon estimation

Carbon content was assumed to be 50% by biomass for trees, saplings, seedlings and roots (Brown, 1997, Nepstad et al., 1994). Litter, woody debris and soil organic carbon was determined by the Walkley-Black method, a wet chemical analysis (Nelson and Sommers, 1996, Walkley and Black, 1934). The Walkley-Black method was reported to underestimate carbon content (Krishan et al., 2009), therefore we used a correction factor of 1.47, developed for Indian soils with similar carbon content to ours (0.22–2%). A carbon content of 42% for fresh litterfall, standing leaf litter and woody debris was used (Burghouts et al., 1992).

### 5.4.13 Statistical analysis and graphical presentation

All statistical analysis and graphical presentation was done in R (R Development Core Team, 2009). We used the *vegan* package (Oksanen, 2009) to calculate $\alpha$ and $\beta$ diversity in logged and unlogged forest. For significance testing we used the *lme* function for linear mixed effects analysis (Pinheiro and Bates, 2000) implemented in the *nlme* package in R 2.9.0 as our experimental design included fixed and random effects. Forest type (logged versus unlogged) was treated as a fixed effect. Replicated transect lines within each forest type (n = 4) were treated as random terms. Within-group heteroscedasticity (increase of variance with the mean) was accounted for by specifying the variance to increase as a power of the primary covariate (i.e. forest type). Mean differences (± 95% CI) in tree diversity, above-ground biomass and

carbon stocks and basal area are reported. For graphical presentation we used the *lattice* package (Sarkar, 2008) and the *graphics* package (Murrell, 2006).

## 5.5 Results

The results presented here for tree diversity and above-ground tree biomass are from data collected in unlogged (Danum Valley) and logged forest (Sabah Biodiversity Experiment). All other components of the carbon budget (above-ground non-tree biomass (including saplings and seedlings), litterfall, litter (including standing leaf litter and woody debris), dead standing wood, below-ground fine roots and soil organic carbon) are estimates from data collected only in logged forest (Sabah Biodiversity Experiment) or from literature estimates (below-ground roots coarse roots).

### 5.5.1 Tree diversity

Fisher's $\alpha$ significantly differed (Mean difference 5.7; with 95% CI = 1.2 to 10.2) between unlogged forest (Mean 34.5; with 95% CI 31.0 to 38.0) and logged forest (Mean 40.2; with 95% CI 37.4 to 43.0) (Fig.9). Our estimates were higher compared to a more comprehensive study for unlogged (Mean $\alpha$ ± 95% CI: 31.4 ± 3.0) and logged forest (30.3 ± 3.7) (Berry et al., 2008). Wittacker's $\beta$ diversity ranged between 0.45 - 0.67 in unlogged forest and between 0.45 - 0.54 in logged forest. We did not detect significant difference in $\beta$ diversity between unlogged and logged forest (Mean difference -0.03; with 95% CI = -0.13 to 0.06). In total we counted 107 species of 37 families in logged forest and 104 species of 35 families in unlogged forest, whereby trees that could not be identified to the species level were counted by there genera only. A recent vegetation survey along seven transect lines (100 m apart, each 750 m long and 20 m wide, total area of 10.5 ha) by the Sabah Forestry Department (2006, unpubl.data) identified up to 180 species of 52 families for the Sabah Biodiversity Experiment, which is currently the best estimate

of tree diversity for this particular site (Table S2). However, it should be noted that this survey aimed at identifying remaining timber stock of the forest stand and was not intended to look at either overall tree diversity or above-ground biomass of individual trees. Out of the trees identified by this study, nine species were classified as either critical (*Hopea nervosa, Parashorea malaanonan, Shorea johorensis*), vulnerable (*Atuna cordata, Cynometra inaequifolia, Eusideroxylon zwagerii*) or endangered (*Dryobalanops lanceolata, Shorea leprosula, Shorea pauciflora*) in the IUCN red list of 2008. These estimates consist only a fraction of the estimated tree species diversity in unlogged forest and logged forest around the Danum Valley Field Station ((Newbery et al., 1992); 511 species in 8 ha unlogged forest, (Bischoff et al., 2005); 307 species in unlogged and 302 species in logged forest of 1.6 ha size, (Berry et al., 2008); 261 species in unlogged and 292 species in logged forest of 1.5 ha size).

With regard to tree density, dipterocarps (87 trees $ha^{-1}$), in particular *Shorea johorensis* (21 trees $ha^{-1}$) and *Shorea parvifolia* (28 trees $ha^{-1}$) were found to be predominant in unlogged forest (Table 2). In logged forest tree densities of dipterocarps declined (69 trees $ha^{-1}$) with no dominance of a single species. In contrast pioneer trees were predominant (89 trees $ha^{-1}$), in particular *Macaranga pearsonii* (24 trees $ha^{-1}$) and *Macaranga gigantea* (23 trees $ha^{-1}$) (Euphorbiaceae), *Neolamarckia cadamba* (33 trees $ha^{-1}$) (Rubiaceae), *Octomeles sumatrana* (4 trees $ha^{-1}$) (Datiscaceae) and *Duabanga moluccana* (5 trees $ha^{-1}$) (Sonneratiaceae) (Table 3).

Basal area significantly differed (Mean difference -4.95 $m^2$ $ha^{-1}$; with 95% CI = -7.54 to -2.35) between unlogged (Mean 29.9; with 95% CI 28.1 to 31.8) and logged forest (Mean 25.0; with 95% CI 22.6 to 27.3). Dipterocarp basal area in logged forest (6.9 $m^2$ $ha^{-1}$ ± 0.2 SEM) was 38% of unlogged forest (18.2 $m^2$ $ha^{-1}$ ± 0.7 SEM). The functional group of pioneer trees, including *Macaranga pearsonii, Macaranga gigantea, Neolamarkia cadamba, Octomeles sumatrana* and *Duabanga moluccana*, dominated the logged

forest in terms of basal area (relative share: 35%), in contrast the species were not observed (<0.2% basal area) in unlogged forest (Table 2 and 3).

### 5.5.2 Carbon baseline estimation

The main carbon stocks were in the trees (Mean ± SEM) (57%; 136 Mg C $ha^{-1}$ ± 7.3), in the soil (25%; 58.2 Mg C $ha^{-1}$ ± 1.3) and in coarse roots (10%; 23.1 Mg C $ha^{-1}$ ± 0.3; literature estimate). Further, dead standing trees (4%; 8.7 Mg C $ha^{-1}$ ± 3.5 SEM) and saplings (2%; 4.8 Mg C $ha^{-1}$ ± 1.7) should be considered as essential parts of an overall budget (Table 1). In total (Mean ± SD) 237.2 Mg C $ha^{-1}$ ± 8.4 was estimated, whereby the above-ground stocks make up 65% and the below ground stocks 35% of the total. Based on an area of 500 ha we predicted a total organic carbon content of (Mean ± SD) 118.6 Gg C ± 4.2 for the Sabah Biodiversity Experiment.

### 5.5.3 Above-ground tree biomass

Tree above-ground biomass stocks were higher in unlogged forest (Mean 468.6 Mg $ha^{-1}$; with 95% CI = 261.6 to 675.6) compared to logged forest (Mean 272.1 Mg $ha^{-1}$; with 95% CI = 225.6 to 318.5) and marginally differed between both (Mean difference -196.5 Mg $ha^{-1}$; with 95% CI = -408.7 to 15.6) (Fig.9). This difference could be attributed to the large canopy trees (>90 cm DBH) that were missing in the logged forest (DBH range: 10.0 - 84.3 cm) compared to unlogged forest (DBH range: 10.1 - 170.3 cm) (Fig.10). Once we removed these 12 trees (>90 cm DBH), mostly *Shorea johorensis* (n = 8), *Shorea parvifolia* (n = 3) and one *Koompassia excelsa*, the difference disappeared and tree above-ground biomass stocks of the unlogged forest were even slightly lower than in the logged

Table 1: Carbon baseline estimation of the Sabah Biodiversity Experiment. Mean (± SEM) are presented for above- and below ground biomass components. Mean (± SD) are presented for the total sum of means (in bold) using a weighted estimate: $\sum_1^k ((k(w_i)s_i^2) / (n_i))$ , where k = # of components, $w_i$ = mean of component / sum of means, $s_i^2$ = variance, $n_i$= number of observations. *Litterfall is not included in the carbon baseline estimation since it is already accounted for by the expansion factor of above-ground tree biomass. C: Carbon. Note that coarse root is a literature estimate (17% of tree above ground biomass).

| | Range | Sample Size (N) | Biomass (Mg ha$^{-1}$) | C Content (%) | C (Mg ha$^{-1}$) | C (%) | Source |
|---|---|---|---|---|---|---|---|
| **Above ground** | | | **323.4 (± 20.2)** | | **155 (± 10.3)** | | |
| Trees | >10cm DBH | 4 transect lines; 1 ha | 272.1 (± 14.6) | 0.5 | 136 (± 7.3) | 57.3 | Forestal International 1973; Pinard 1996 |
| Saplings | >2m height, <10 cm DBH | 24 (each 25 m$^2$ quadrate) | 9.5 (± 3.4) | 0.5 | 4.8 (± 1.7) | 2.0 | Own data |
| Seedlings | <2m height | | 0.6 (± 0.2) | 0.5 | 0.3 (± 0.1) | 0.1 | Own data |
| Litterfall* | Leaves, small twigs (>1cm diameter), reproductive organs | 40 (25 collection dates) | 11.7 (± 0.3) | 0.42 | 4.9 (± 0.1) | included in above ground estimates | Own data; C content (Burghouts et al. 1992) |
| **Necromass** | | | | | | | |
| Standing litter | | 24 (each 25 m$^2$ quadrate) | 1.6 (± 0.3) | 0.42 | 0.7 (± 0.1) | 0.3 | Own data; C content (Burghouts et al. 1992) |
| Woody debris | | | 10.6 (± 4.4) | 0.42 | 4.5 (± 1.8) | 1.9 | Own data; C content (Burghouts et al. 1992) |
| Dead standing trees | | 4 transect lines; 1 ha | 17.3 (± 7.0) | 0.5 | 8.7 (± 3.5) | 3.7 | Own data, wood density estimate Delaney (1998) |
| **Below ground** | | | **48.2 (± 0.9)** | | **82.2 (± 1.0)** | | |
| Coarse root | >5mm diameter | 4 transect lines | 46.3 (± 0.6) | 0.5 | 23.1 (± 0.3) | 9.7 | Pinard 1997 |
| Fine root | (≤2 mm diameter) 0–5cm depth (topsoil) | 24 (each 25 m$^2$ quadrate) | 1.9 (± 0.2) | 0.5 | 0.9 (± 0.1) | 0.4 | Own data |
| Soil organic carbon | ≤ 1m depth | 396 (12 plots, 11 layers, 3 replicates) | – | 0.27 - 0.99 | 58.2 (± 1.3) | 24.5 | Own data; correction factor 1.47 (Krishan et al. 2009) |
| **Total** | | | **371.6 (± 18.9)** | | **237.2 (± 8.4)** | **100** | |

Table 2: Overview of the most important tree families and species (>10 cm DBH) in unlogged forest. BA: Mean (± SEM) Basal Area, DBH: Diameter at Breast Height (1.3 m).

| Family | Species | BA ($m^2$ $ha^{-1}$) | BA (%) | DBH range (cm) | Tree density ($ha^{-1}$) |
|---|---|---|---|---|---|
| **Dipterocarpaceae** | | **18.24 (± 0.66)** | **61.0** | **10.1 – 170.3** | **87** |
| | *Shorea johorensis* | 9.09 (± 0.67) | 30.4 | 10.5 – 170.3 | 21 |
| | *Shorea parvifolia* | 6.22 (± 0.09) | 20.8 | 11.7 – 116.3 | 28 |
| | *Parashorea malaanonan* | 1.61 (± 0.26) | 5.4 | 10.6 – 67.2 | 12 |
| | *Hopea nervosa* | 0.99 (± 0.11) | 3.3 | 10.1 – 47.5 | 17 |
| **Meliaceae** | | **1.91 (± 0.11)** | **6.4** | **10.0 – 32.3** | **61** |
| | *Chisocheton sarawakensis* | 0.55 (± 0.04) | 1.8 | 10.0 – 30.0 | 17 |
| | *Aglaia elliptica* | 0.45 (± 0.02) | 1.5 | 10.1 – 31.8 | 15 |
| | *Aglaia macrocarpa* | 0.39 (± 0.03) | 1.3 | 11.4 – 31.0 | 10 |
| **Leguminosae** | | **1.89 (± 0.40)** | **6.3** | **10.0 – 144.8** | **6** |
| | *Koompassia excelsa* | 1.65 (± 0.41) | 5.6 | 144.8 | 1 |
| **Lauraceae** | | **1.33 (± 0.09)** | **4.4** | **10.0 – 45.6** | **44** |
| **Euphorbiaceae** | | **1.13 (± 0.08)** | **3.8** | **20.0 – 36.1** | **61** |
| **Myrtaceae** | | **0.98 (± 0.13)** | **3.3** | **10.7 – 57.1** | **19** |
| | *Syzygium fastigiatum* | 0.63 (± 0.12) | 2.1 | 14.1 – 57.1 | 5 |
| **Tiliaceae** | | **0.76 (± 0.08)** | **2.5** | **10.0 – 43.1** | **21** |
| | *Pentace laxiflora* | 0.65 (± 0.08) | 2.2 | 11.4 – 43.1 | 15 |
| **Fagaceae** | | **0.62 (± 0.06)** | **2.1** | **11.7 – 50.5** | **10** |
| **Burseraceae** | | **0.38 (± 0.03)** | **1.3** | **10.6 – 41.4** | **11** |
| **Others** | | **2.67 (± 0.04)** | **8.9** | **10 – 52.0** | **99** |
| **Total** | | **29.91 (± 0.66)** | **100** | **10 – 170.3** | **410** |

Table 3: Overview of the most important tree families and species (>10 cm DBH) in logged forest. BA: Mean (± SEM) Basal Area, DBH: Diameter at Breast Height (1.3 m).

| Family | Species | BA ($m^2$ $ha^{-1}$) | BA (%) | DBH range (cm) | Tree density ($ha^{-1}$) |
|---|---|---|---|---|---|
| **Dipterocarpaceae** | | **6.88 (± 0.17)** | **27.6** | **10.0 – 84.3** | **69** |
| | *Shorea johorensis* | 1.61 (± 0.17) | 6.4 | 13.8 – 84.3 | 7 |
| | *Shorea gibbosa* | 1.54 (± 0.14) | 6.2 | 10.6 – 72.5 | 13 |
| | *Dryobalanops lanceolata* | 0.86 (± 0.08) | 3.4 | 12.8 – 72.1 | 7 |
| | *Shorea fallax* | 0.67 (± 0.17) | 2.7 | 13.4 – 71.0 | 3 |
| | *Dipterocarpus caudiferus* | 0.59 (± 0.10) | 2.4 | 9.8 – 60.5 | 10 |
| **Euphorbiaceae** | | **5.42 (± 0.24)** | **21.7** | **10.0 – 64.0** | **107** |
| | *Macaranga pearsonii* | 2.75 (± 0.21) | 11.0 | 17.0 – 64.0 | 24 |
| | *Macaranga gigantea* | 1.29 (± 0.05) | 5.2 | 13.0 – 38.8 | 23 |
| **Rubiaceae** | | **3.79 (± 0.16)** | **15.2** | **10.0 – 48.0** | **74** |
| | *Neolamarckia cadamba* | 3.11 (± 0.13) | 12.4 | 10.2 – 48.0 | 33 |
| **Leguminosae** | | **0.84 (± 0.10)** | **3.4** | **10.3 – 72.8** | **14** |
| **Datiscaceae*** | | **0.79 (± 0.16)** | **3.2** | **23.8 – 80.9** | **4** |
| | *Octomeles sumatrana* | 0.79 (± 0.16) | 3.2 | 23.8 – 80.9 | 4 |
| **Lauraceae** | | **0.75 (± 0.07)** | **3.0** | **11.1 – 59.8** | **12** |
| **Sonneratiaceae*** | | **0.71 (± 0.14)** | **2.8** | **14.2 – 77.2** | **5** |
| | *Duabanga moluccana* | 0.71 (± 0.14) | 2.8 | 14.2 – 77.2 | 5 |
| **Sapindaceae** | | **0.55 (± 0.06)** | **2.2** | **16.5 – 51.2** | **8** |
| **Tiliaceae** | | **0.54 (±0.07)** | **2.2** | **11.5 – 62.1** | **8** |
| **Others** | | **4.69 (± 0.13)** | **18.8** | **10.0 – 59.1** | **116** |
| **Total** | | **24.96 (± 0.83)** | **100** | **10.0 – 84.3** | **417** |

forest (Mean difference -50.6 Mg $ha^{-1}$; with 95% CI -149.8 to 48.7). Further, tree biomass stocks were more evenly distributed in logged forest compared to unlogged forest as shown by the difference in variance (Fig.9). Total biomass in logged forest was estimated at 372 Mg $ha^{-1}$, where above-ground biomass stocks (87%) were higher than below ground stocks (13%) (Table 1). Live trees contributed to 84% of the above-ground biomass. If we included standing deadwood (5%) the overall contribution of all trees to total above-ground biomass was as high as 89%. In total we calculated (Mean ± SEM) 48.6 ± 10.2 dead stems $ha^{-1}$ with a mean volume of 34.6 ± 14.1 $m^3$ $ha^{-1}$, indicating that this pool is important to consider for an overall carbon budget.

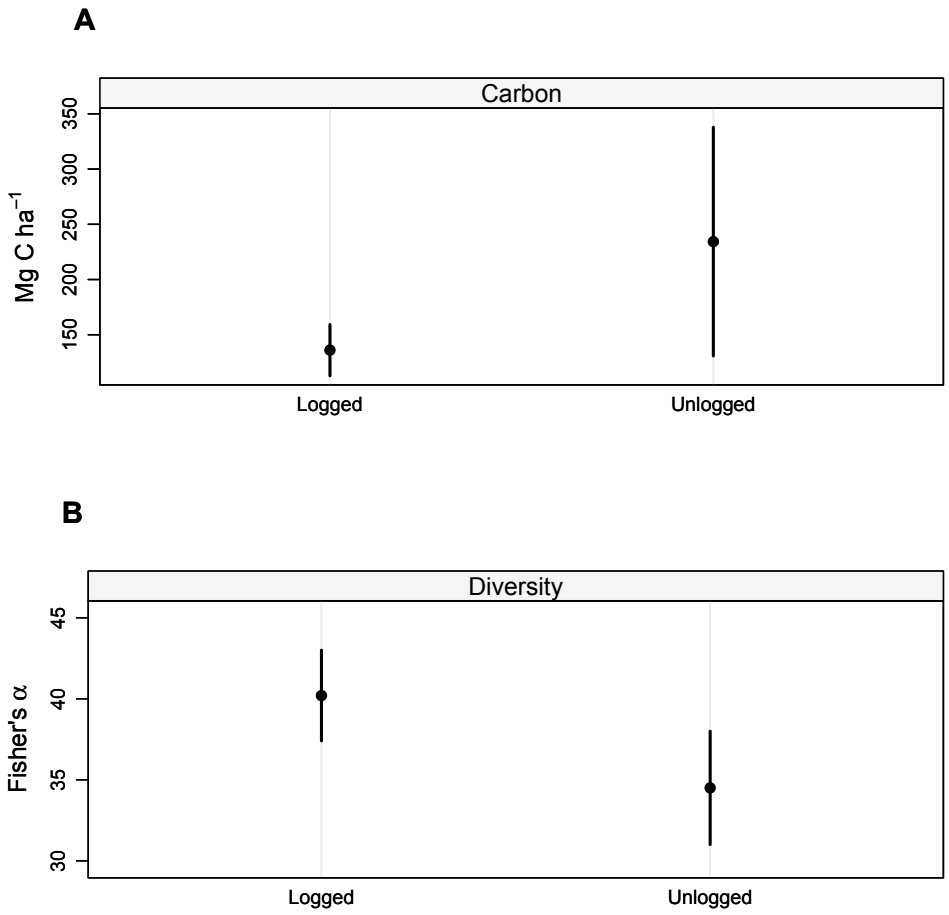


Figure 9 (A) Carbon stocks (50% tree biomass) and (B) diversity estimates for trees >10 cm DBH (Diameter Breast Height). Mean (± 2.8 SEM (95% CI)) are shown for logged (Sabah Biodiversity Experiment) and unlogged (Danum Valley) forest. Fisher's α estimates the number of tree species represented by a single individual.

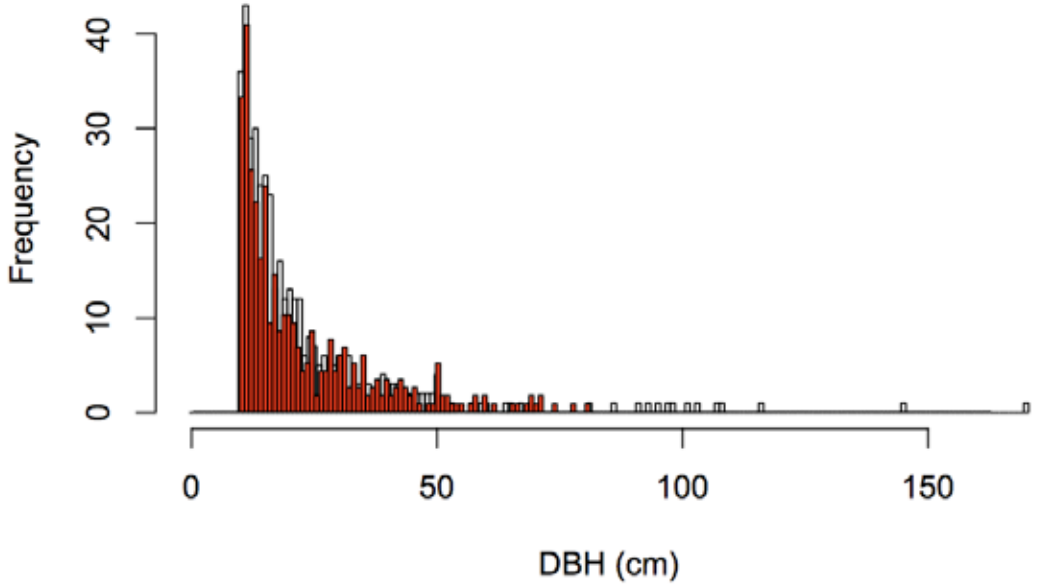


Figure 10 Tree DBH (>10 cm Diameter Breast Height) for logged (red; Sabah Biodiversity Experiment) and unlogged forest (white; Danum Valley). Note the difference in frequency distribution for tree DBH > 90 cm.

### 5.5.4 Above-ground non-tree biomass

We measured a mean dipterocarp sapling (<10 cm DBH and >2m height) and seedling (<2m height) density of 800 ± 240 (SEM) $ha^{-1}$ in the logged forest of the Sabah Biodiversity Experiment. This estimate does not include enrichment planted saplings and seedlings. Dipterocarp saplings and seedlings of ten species were identified in an area of 600 $m^2$ (n = 24, each quadrat 25 $m^2$). This indicates that the density but not the diversity of the sapling and seedling stock was high in the plots measured. Total basal area of all dipterocarp saplings and seedlings in the study area was estimated at 0.46 $m^2$ $ha^{-1}$.

### 5.5.5 Litterfall

Fine litterfall rate, including leaves, small twigs (<1 cm DBH) and reproductive organs, was (Mean ± SEM) 11.7 ± 0.3 t $ha^{-1}$ $yr^{-1}$. Considering leaf litter only, the total amount was 7.6 ± 0.4 Mg $ha^{-1}$ $yr^{-1}$. Litter-

fall rates varied significantly between collection dates (n = 25) (Fig.11). Peaks in litterfall occurred during the months of August (1.3 ± 0.1 Mg ha$^{-1}$ month$^{-1}$) and May (1.4 ± 0.2 Mg ha$^{-1}$ month$^{-1}$). In both months mean rainfall was exceptionally high, even though these months are during the inter-monsoon, which is generally drier. Lowest litterfall rates occured in September (0.6 ± 0.1 Mg ha$^{-1}$ month$^{-1}$) and February (0.5 ± 0.2 Mg ha$^{-1}$ month$^{-1}$). Litterfall in our study was independent of the Northeast monsoon from November to March or the Southwest monsoon during June and July, when generally higher precipitation is expected (Marsh and Greer, 1992) (Fig.11). Overall there was no apparent seasonal trend in litterfall determinable. Changes in litterfall rates were also not related to rainfall, which is recognized as the most important driver of ecosystem processes in aseasonal regions (Burghouts et al., 1992).

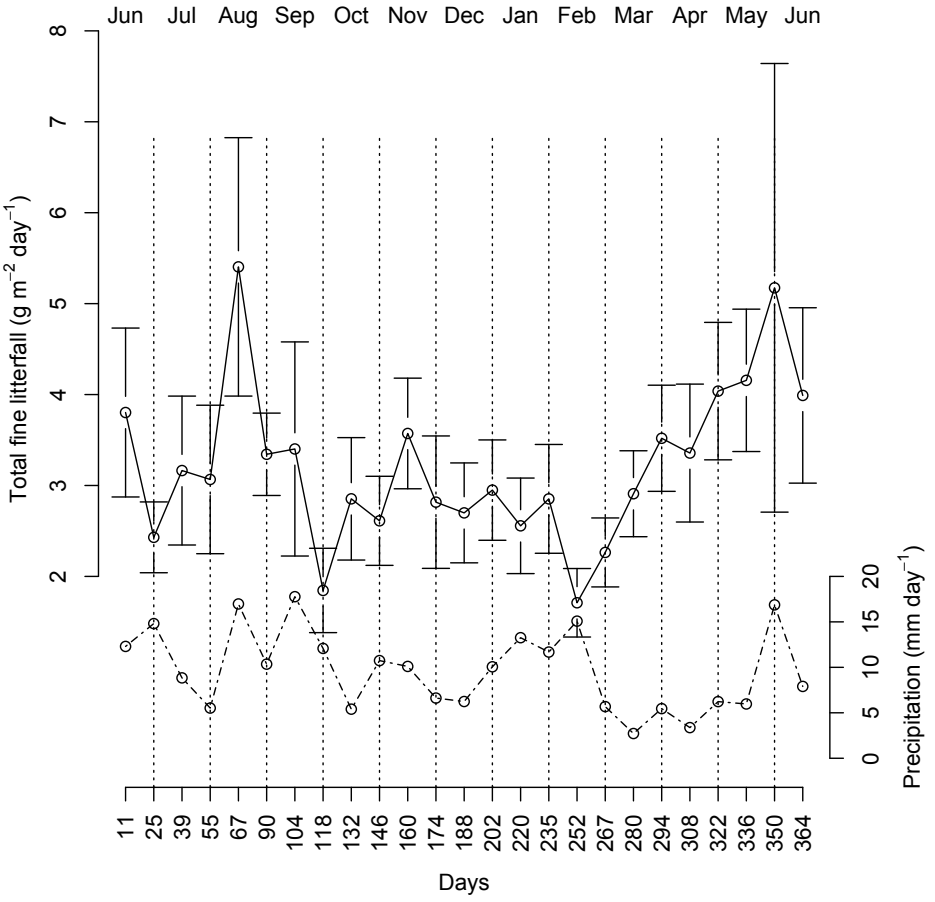


Figure 11 Time series of total fine litterfall (solid line; Mean ± 2 SEM) and precipitation (dashed line; Mean). Days indicate litter collections (n = 25) in 2006/07. Mean litterfall and rainfall were calculated over the fourteen days prior to collection.

### 5.5.6 Soil organic carbon

Soil organic carbon was estimated from thirteen randomly located sites of the logged forest (Sabah Biodiversity Experiment). Soil bulk density (Mean ± SEM; 1.07 g $cm^{-3}$ ± 0.07) was marginally lower in the top soil of logged forest (< 0.1 m) (0.93 g $cm^{-3}$ ± 0.05) compared to 0.1 to 1 m depth (1.11 g $cm^{-3}$ ± 0.07). Soil organic carbon content was significantly higher in the top 0.2 m (Mean ± SEM; 0.99% ± 0.18) and consistent from 0.2 to 1 m soil depth (0.27% ± 0.05) (Fig.12). Mean soil organic carbon content was relatively low across all sites (Mean ± SEM) (58.2 Mg $ha^{-1}$ ± 1.3). Highest concentrations of soil organic carbon were found in the top 0.2 m of the soil (8.43 Mg $ha^{-1}$ ± 0.3), in the sub-soil (0.2 - 1 m depth) levels decreased to 4.1 Mg $ha^{-1}$ ± 0.3.

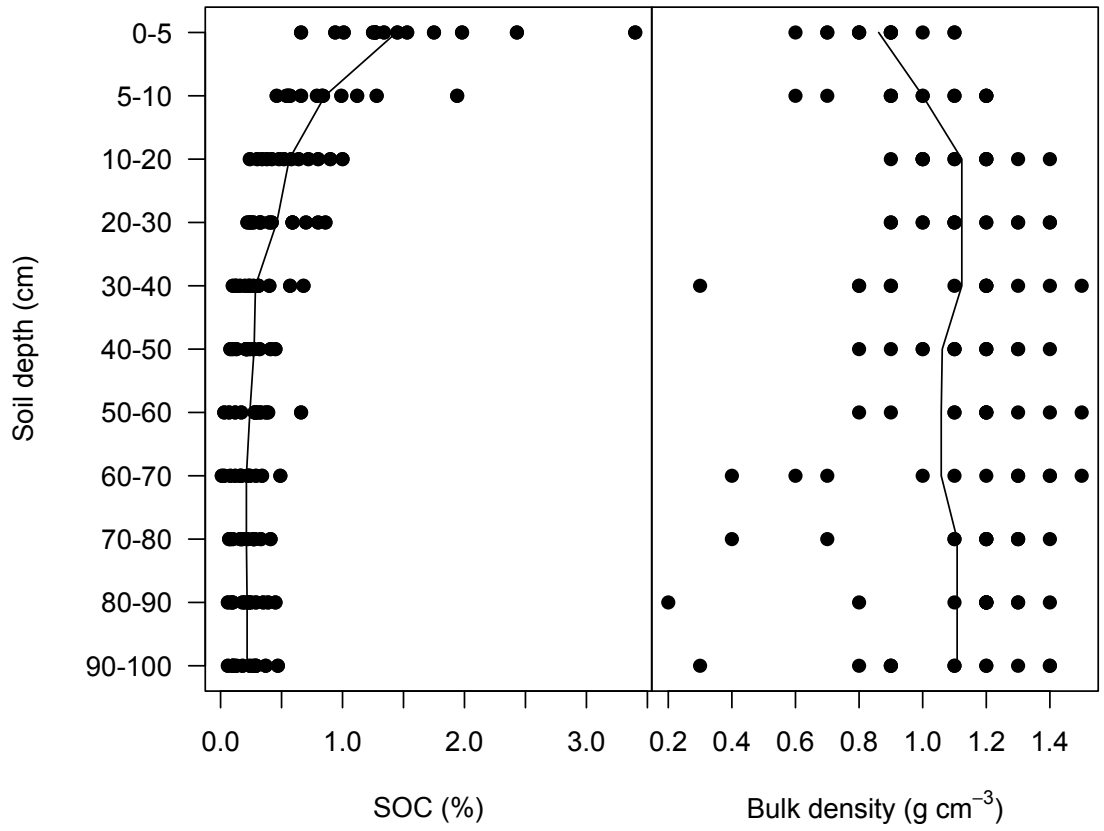


Figure 12 Soil organic carbon content (SOC (%)) and bulk density values (g $cm^{-3}$) in soil layers of the logged forest (Sabah Biodiversity Experiment) down to 1 m depth. A locally weighted regression (solid line) was fitted for ease of graphical interpretation

## 5.6 Discussion

### 5.6.1 Tree carbon storage

The main results of the comparison between the two forest types are a lower above-ground tree biomass and a higher tree α diversity in logged forest compared to unlogged forest. The observed patterns of both are not directly (causally) related and measured differences are expected to be a consequence of logging operation or regional differences in vegetation composition. With regard to carbon storage we found that trees are the most important pool to consider. Tree above-ground biomass and associated carbon stocks were found to be higher in unlogged forest compared to logged forest. These findings indicate that 30 year old logged forest still holds depleted tree carbon stocks. The difference could be attributed to the missing large trees (>90 cm DBH), and in particular the missing large dipterocarps in the logged forest. When considering the basal area ($m^2$ $ha^{-1}$) of particular tree families, we do find that dipterocarps are dominant in both unlogged and logged forest as found in other studies (Cannon et al., 1998). In contrast, when considering functional groups of trees, pioneer trees dominated the logged forest in terms of basal area. The indicator species of disturbance for the logged forest of the Sabah Biodiversity Experiment are *Macaranga pearsonii* and *Macaranga gigantea* (both ranked at a score of 60 (0 = low disturbance, 100 = high disturbance (Slik et al., 2003)). The high abundance of these species in the logged forest suggests that the forest should be classified as heavily disturbed secondary forest. Both species are considered as typical pioneer trees for lowland mixed dipterocarp forest (Davies et al., 1998, Slik et al., 2000). Further they are in particular found in conventionally logged forest (Sist and Nguyen-The, 2002). The density of pioneer trees (>10 cm DBH) in the Sabah Biodiversity Experiment (89 $ha^{-1}$) is comparable to other reports from closeby secondary forest (8 years post logging: 92 $ha^{-1}$) and (13 years post logging: 76 $ha^{-1}$) (Bischoff et al., 2005). As pioneers are typically light demanding, fast growing and have a lower wood density this may explain to some part the observed difference in above-ground tree biomass between logged and unlogged

forest. Dipterocarp basal area was found to decrease to a third from unlogged (61%; 18.24 $m^2$ $ha^{-1}$) to logged (28%; 6.88 $m^2$ $ha^{-1}$) forest similar to results of Berry et al. (2008). The relative share in basal area of the five most important pioneer species in logged forest was consistent with this observation (35%; 8.65 $m^2$ $ha^{-1}$) as they contributed <0.2% of basal area in unlogged forest (Table 3). We therefore hypothesise the occurence of competitive release, suggesting that big trees suppress other vegetation, once they are removed the vegetation composition may change. According to simulation studies of the Deramakot forest reserve, pioneers were expected to dominate logged-over forest for up to 50 years (Huth and Tietjen, 2007). After they die out climax species are expected to overtake the forest structure and wood volumes (approximately 500 $m^3$ $ha^{-1}$) of undisturbed forests were predicted after 80 years. Further it was expected that the complete forest structure including species group composition is reached 200 years after logging (Huth and Tietjen, 2007). Silvicultural treatments may therefore be necessary to improve dipterocarp carbon stocks to prelogging levels, as was done for the Sabah Biodiversity Experiment since 2000 with the line enrichment planting. Nabuurs and Mohren (1993) estimated on the basis of model outputs that approximately 80 Mg C $ha^{-1}$ can be stored additionally by this method. For the Sabah Biodiversity Experiment we therefore expect an increase in tree above-ground carbon stocks of approximately 60% (baseline 136 Mg $ha^{-1}$ ± 7.3).

### 5.6.2 Tree diversity

With regard to tree α diversity we expected that the loss of dipterocarps lowers diversity in logged forest, which could not be confirmed. Previous studies have reported similar levels of tree diversity in Bornean logged forests compared to unlogged forest (Cannon et al., 1998, Kitayama et al., 2006, Berry et al., 2008). Based on these findings they argue that degraded forests can maintain tree diversity levels compared to unlogged forest and should therefore be reassessed for their conservation value. However, the

higher tree α diversity observed in the logged forest of this study is more likely to be an artifact from insufficient area sampled (1 ha over a 10 ha area in both logged and unlogged forest) and should be interpreted with care (Ashton 2008). To what extent degraded forest can maintain both, tree diversity levels and carbon storage, is not well understood for tropical forests and more experimental evidence is needed (Erskine et al., 2006, Potvin and Dutilleul, 2009). Only few recent observational studies could be found that addressed the relationship between above-ground biomass and tree diversity for Borneo (Seino et al., 2006, Slik et al., 2008). Both studies suggested that degraded forest can recover above-ground biomass and tree diversity if sustainable forest management practices are pursued (Seino et al., 2006) or if burned forests are protected from further anthropogenic changes (Slik et al., 2008). Other studies either focus on tree diversity (Cannon et al., 1998, Foody and Cutler, 2003, Bischoff et al., 2005, Kohler and Huth, 2007, Berry et al., 2008) or on carbon storage (Pinard and Putz, 1996, Putz et al., 2008, Lasco et al., 2006) separately.

The use of remote sensing is a promising approach to relate stand diversity levels, in terms of species number, evenness and composition, to biomass estimations of forests (Griffiths et al., 2000, Drake et al., 2002, Drake et al., 2003, Lefsky et al., 2005). One aspect to address is the importance of autocorrelation, which has not been considered as part of this study. To date the translation of spectral differences to tree diversity is difficult for tropical forests, however reliable predictions of forest biomass could be shown at the landscape level for North Borneo (Foody et al., 2001, Kitayama et al., 2006, Tangki and Chappell, 2008). Further, it was shown that ground based measurements are still essential to validate outputs of remote sensing data for tropical forest biomass estimation, since accuracy declined when applied to new regions (Foody and Cutler, 2003). Here we provide such initial measurements for 30 year old logged forest that can be further incorporated into more extensive studies.

### 5.6.3 Carbon baseline estimation

Several studies have published estimates of carbon stocks across South-East Asia (see Nabuurs and Mohren 1993 or Lasco and Pulhin 2004 for a review). Estimates for old growth forest range from 182 Mg C $ha^{-1}$ in Thailand (Boonpragob, 1998), 201 Mg C $ha^{-1}$ in the Philippines (Lasco et al., 2000) and 390 Mg C $ha^{-1}$ in Indonesia (Hairiah and Sitompul, 2000). For Peninsular Malaysia estimates are in the range of 360 Mg C $ha^{-1}$ for undisturbed mixed dipterocarp forest, and 230 Mg C $ha^{-1}$ for disturbed forest (Abu Bakar, 2000). For Sarawak we could only find estimates for above-ground biomass and tree volume: 280-405 Mg $ha^{-1}$ (Brown et al., 1991) and 464 $m^3$ $ha^{-1}$ respectively (Ashton and Hall, 1992). Estimates from Sabah largely reflected the work of Pinard (1996, 1997), where they reported a prelogging carbon density of 261 Mg C $ha^{-1}$, including total biomass of (Mean ± SEM) 200 Mg C $ha^{-1}$ ± 10, woody debris and litter (28 Mg C $ha^{-1}$) and soil organic matter (33 Mg C $ha^{-1}$) for selected sites in the Ulu Segama Forest Reserve. Tangki and Chappell (2008) used the same allometries (Forestal International Limited, 1973) and similar sites in the Ulu Segama Forest Reserve to estimate tree biomass by remote sensing. They quantified tree biomass at 506 Mg $ha^{-1}$ ± 60 for unlogged forest and 192 Mg $ha^{-1}$ ± 96 for approximately 25 year old conventional logged forest. Seino et al. (2005) reported aboveground biomass estimates of 482-522 Mg $ha^{-1}$ for primary forest and even higher levels for 40 year old logged forest of the Deramakot Forest Reserve (483-596 Mg $ha^{-1}$). Such large differences are likely to be explained by the use of a different allometric model (Brown, 1997).

A major obstacle in measuring carbon stocks and changes thereof is the high spatial and vertical heterogeneity of soil carbon (Don, 2007). Even more so if we consider that forest cover usually slows erosion (Leigh, 1999) and soil carbon concentrations therefore could depend on previous logging intensity. In temperate forests about 50-70% of the carbon is stored as soil organic carbon (Dixon et al., 1994). For the system under study we expected to measure carbon stocks in the range of 58 - 104 Mg C $ha^{-1}$ (Bremen

et al., 1990). Our estimates were low compared to other studies, indicating that the soil was heavily disturbed and did not recover well over 30 years. Even though we surveyed a large area (500 ha) with point samples (three replicates per sample) we found that both, bulk density and soil organic carbon contents were relatively consistent (Fig.12), suggesting that our estimates may be representative for the study area. Soil organic carbon estimates should be considered with care, in particular when measured with the Walkley-Black method which generally underestimates carbon content (Krishan et al., 2009).

Carbon pools that are directly related to soil organic carbon turnover rates but also to forest disturbance include dead standing trees and coarse woody debris, fine root biomass and litterfall. All these pools were previously studied in unlogged primary forest of the Danum Valley Conservation Area (Green, 1992, Green et al., 2005, Gale, 2000, Burghouts et al., 1992, Burghouts et al., 1998). Compared to our estimates from logged forest, both, standing volume (Mean ± SEM; 34.6 ± 14.1 $m^3$ $ha^{-1}$) and basal area (6.0 ± 0.3 $m^2$ $ha^{-1}$) of dead standing trees were not significantly different compared to findings from unlogged forest at Danum Valley (25.8 ± 4.3 $m^3$ $ha^{-1}$ and 5.6 ± 0.5 $m^2$ $ha^{-1}$ respectively) (Gale, 2000). In contrast, downed volume (fallen trees and branches lying on the ground) was estimated to be much higher in their study (70.6 ± 9.5 $m^3$ $ha^{-1}$) compared to ours (20.6 ± 8.8 $m^3$ $ha^{-1}$). The low estimate of our study is surprising, since a heavy storm in 2007 caused major tree and branchfalls (pers. observ.). This may indicate that our method of collecting all woody debris within 24 subquadrats (0.5 x 0.5 $m^2$) did not capture large downed woody debris adequately and that other proposed methods should be considered (von Oheimb et al., 2007, Wirth and von Oheimb, unpubl.). The most comprehensive work on fine root distribution of the area under study was done by Green (1992), later published in Green et al. (2005). He estimated fine root biomass (≤2 mm diameter) in the top 1.2 m of undisturbed forest soil at 2.83 Mg $ha^{-1}$ and fine root production and disappearance as 4.02 and 4.84 Mg $ha^{-1}$ $yr^{-1}$. Fine root biomass between 0-15 cm soil depth was later published as (Mean ± SEM; 1.70 Mg $ha^{-1}$ ± 0.04) (Green et al., 2005). Our estimation

was not significantly different (1.9 Mg $ha^{-1}$ ± 0.2), despite the fact that we took fine roots down to 5 cm soil depth only. Burghouts et al. (1992, 1994, 1998) compared spatial and temporal litterfall rates of 15 year old logged forest and unlogged forest. Total litterfall (including leaf, twigs, woody and fragmented litterfall) was estimated at (Mean ± SEM) 11.1 Mg $ha^{-1}$ $yr^{-1}$ ± 0.33 for unlogged forest and 11.5 Mg $ha^{-1}$ $yr^{-1}$ ± 0.31 for logged forest (see Table 1 of Burghouts et al. 1992). Litterfall rates from our studies were again not significantly different from either of their reported estimates.

Even though we cannot directly infer the forest condition of the Sabah Biodiversity Experiment, estimates of coarse woody debris, fine root biomass and litterfall were found to be similar to unlogged forest, suggesting that 30 year old logged forest can fully maintain these ecosystem processes. Clearly more extensive research on any of these pools should be undertaken in the future to draw a more complete picture of the carbon pools present in the Sabah Biodiversity Experiment. In particular the three major pools (above-ground tree biomass, coarse root biomass and soil organic carbon)—which cover over 90% of the stored carbon—were estimated based on allometric equations and correction factor derived elsewhere (Forestal International Limited, 1973, Krishan et al., 2009, Pinard, 1995) and should be estimated with greater precision. Despite these limitations we applied our carbon baseline estimation from logged forest to unlogged forest to compare the estimate against previous predictions. Assuming that aside from tree above-ground carbon stocks all carbon pools are similar, the estimate is 601 Mg $ha^{-1}$ ± 20.0 for total biomass and 335.5 Mg C $ha^{-1}$ ± 9.2 for total carbon stocks. These estimates are 34% higher than what was previously proposed for unlogged forest of the Ulu Segama Forest Reserve (Pinard and Putz, 1996), but they are close to back calculations from model predictions (625 Mg $ha^{-1}$) for dry biomass in virgin tropical forest of good soil fertility (Nabuurs and Mohren, 1993). With regard to the low soil carbon pool in this study the total carbon stock for unlogged forest is likely to be even higher than proposed here.

In summary we found that tree above-ground carbon stocks and tree α diversity significantly differed between logged forest of the Sabah Biodiversity Experiment compared to unlogged forest at Danum Valley. Despite the broad approach our estimates of a carbon baseline, covering all six major carbon pools, were comparable to more exhaustive measures on individual carbon pools of previously published studies. In particular possible indicators of forest quality (dead standing wood, fine roots and litterfall) revealed that our study area may provide some fundamental ecosystem processes at similar rates compared to unlogged forest. More extensive work on the relation between carbon storage and tree diversity is needed in the future, including comparative studies from primary forest, logged forest, fragmented forest areas and oil palm (*Elaeis guineensis*) plantations, to draw better conclusions about the causal relationship between tree diversity and related ecosystem processes in tropical forests of Borneo.

## 5.7 Acknowledgements

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# 5.8 Appendix

Table S1: Overview of height and volume allometries for calculation of tree biomass in logged and unlogged forest. For details see Pinard (1996). No: Indicates timber groupings (see Table S2 for details), H: Height Allometry based on DBH (D) measurements. N: Sample size, V: Volume Allometry based on DBH (D) measurements

| No | Height | N | $R^2$ | Stem volume | N | $R^2$ |
|---|---|---|---|---|---|---|
| **1** | $H= 5.506+0.4119*D-0.00162*(D^2)$ | 151 | 0.84 | $V= 0.038+0.0053*((D^2)*H)/100$ | 91 | 0.99 |
| **2** | $H= 2.614+0.5529*D-0.00302*(D^2)$ | 262 | 0.85 | $V= 0.1532+0.005*((D^2)*H)/100$ | 172 | 0.99 |
| **3** | $H= -0.3622+0.6403*D-0.00337*(D^2)$ | 275 | 0.88 | $V= -0.0362+0.005*((D^2)*H)/100+0.00000005*(((D2)*H)/100)^2$ | 98 | 0.99 |
| **4** | $H= -0.3152+0.7511*D-0.00429*(D^2)$ | 145 | 0.88 | $V= -0.0364+0.005*((D^2)*H)/100$ | 94 | 0.99 |
| **5** | $H= 2.517+0.5997*D-0.00322*(D^2)$ | 136 | 0.85 | $V= 0.164+0.0041*((D^2)*H)/100+0.00000041*(((D2)*H)/100)^2$ | 96 | 0.99 |
| **6** | $H= 5.0849+0.33498*D-0.00102*(D^2)$ | 162 | 0.86 | $V= 0.1363+0.0046*((D^2)*H)/100+0.00000007*(((D2)*H)/100)^2$ | 83 | 0.99 |
| **7** | $H= 3.999+0.425*D-0.00195*(D^2)$ | 200 | 0.79 | $V= 0.1292+0.0047*((D^2)*H)/100+0.00000015*(((D2)*H)/100)^2$ | 90 | 0.99 |
| **8** | $H= 2.528+0.3635*D-0.0019*(D^2)$ | 666 | 0.75 | $V= 0.0582+0.0048*((D^2)*H)/100$ | 142 | 0.99 |
| **9** | $H= 2.297+0.3304*D-0.00144*(D^2)$ | 638 | 0.76 | $V= -0.0145+0.0056*((D^2)*H)/100$ | 131 | 0.99 |
| **10** | $H= 3.981+0.2848*D-0.00119*(D^2)$ | 509 | 0.71 | $V= 0.0322+0.0054*((D^2)*H)/100$ | 49 | 0.99 |
| **11** | $H= 2.056+0.4659*D-0.00221*(D^2)$ | 141 | 0.89 | $V= -0.0195+0.0047*((D^2)*H)/100$ | 47 | 0.99 |
| **12** | $H= 11.46+0.263*D-0.00114*(D^2)$ | 50 | 0.72 | $V= -0.1918+0.0058*((D^2)*H)/100$ | 23 | 0.99 |
| **13** | $H= 3.497+0.238*D-0.00152*(D^2)$ | 189 | 0.62 | $V= -0.0547+0.0053*((D^2)*H)/100$ | 49 | 0.99 |
| **14** | $H= -3.189+0.7358*D-0.00472*(D^2)$ | 316 | 0.88 | $V= 0.02997+0.0039*((D^2)*H)/100+0.00000018*(((D2)*H/100)^2$ | 48 | 0.99 |
| **15** | $H= 3.329+0.2638*D-0.00136*(D^2)$ | 343 | 0.68 | $V= -0.0021+0.0051*((D^2)*H)/100$ | 79 | 0.99 |

Table S2: Trees (>10 cm DBH) of the pre-existing logged forest of the Sabah Biodiversity Experiment identified to species or genus level. No: Functional grouping for allometric equation (see Table S1). Wood Density: From the World Agroforestry Centre Wood Density Database. IUCN Status (2008): Critical (CR), Vulnerable (VU), Endangered (EN). Tree Guilds: Non-pioneer (NP), pioneer (P), based on family level estimation of plant taxonomic expert (Bernardos, pers.comm.).

| No | Family | Botanical name | Wood Density ($g\ cm^{-3}$) | IUCN Status | Guild |
|---|---|---|---|---|---|
| 15 | Lauraceae | *Actinodaphne sp.* | 622.5 | | NP |
| 15 | Theaceae | *Adinandra myreniura* | 695 | | |
| 8 | Meliaceae | *Aglaia macrocarpa* Miq. | 687.5 | | NP |
| 8 | Meliaceae | *Aglaia odoratissima* Bl. | 885 | | NP |
| 8 | Meliaceae | *Aglaia squamulosa* King | 785 | | NP |
| 15 | Alangiaceae | *Alangium griffithii* Harms | 870 | | |
| 15 | Alangiaceae | *Alangium javanicum* (Bl) Wangerin | 875 | | |
| 15 | Lauraceae | *Alseodaphne sp.* | 630 | | NP |
| 15 | Euphorbiaceae | *Aporusa accuminatissima* Merr. | 730 | | |
| 15 | Euphorbiaceae | *Aporusa elmerii* Merr. | 730 | | |
| 15 | Euphorbiaceae | *Aporusa grandistipula* Merr. | 730 | | |
| 15 | Thymelaeaceae | *Aquilaria malaccensis* Lamk. | 400 | VU | |
| 8 | Leguminosae | *Archidendron sp.* | 605 | | |
| 15 | Myrsinaceae | *Ardisia sp.* | 510 | | |
| 15 | Moraceae | *Artocarpus anisophyllus* Miq. | 740 | | |
| 15 | Chrysobalanaceae | *Atuna cordata* Cockburn ex Prance | 842.5 | VU | |
| 15 | Meliaceae | *Azadiracta excelsa* Jacobs | 600 | | NP |
| 15 | Euphorbiaceae | *Baccaurea stipulata* J.J. Smith | 792.5 | | |
| 15 | Euphorbiaceae | *Baccaurea tetandra* | 796 | | |
| 15 | Lecythidaceae | *Barringtonia macrostachya* Jack | 647.5 | | |
| 15 | Lauraceae | *Beilschmiedia sp.* | 622.5 | | NP |
| 15 | Euphorbiaceae | *Blumeodendron tokbrai* J.J. Smith | 645 | | |
| 15 | Tiliaceae | *Brownlowia peltata* Benth. | 595 | | NP |
| 15 | Anacardiaceae | *Buchanania sessilifolia* Bl. | 505 | | |
| 15 | Labiatae | *Callicarpa sp.* | 410 | | |
| 15 | Guttiferae | *Calophyllum sp.* | 680 | | |
| 15 | Theaceae | *Camellia sp.* | 619 | | |
| 10 | Burseraceae | *Canarium denticulatum* Bl. | 625 | | |
| 10 | Burseraceae | *Canarium odontophyllum* Miq. | 635 | | |
| 9 | Fagaceae | *Castanopsis sp.* | 762.5 | | |
| 15 | Olacaceae | *Chionanthus sp.* | 672.5 | | NP |
| 8 | Meliaceae | *Chisocheton sp.* | 712.5 | | NP |
| 15 | Lauraceae | *Cinnamomum sp.* | 430 | | NP |
| 15 | Euphorbiaceae | *Cleistanthus myrianthus* Kurz | 720 | | |
| 15 | Euphorbiaceae | *Cleistanthus paxii* Jabl. | 685 | | |
| 15 | Euphorbiaceae | *Clorophyllum wallichinum* | 830 | | |

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|---|---|---|---|---|---|
| 15 | Guttiferae | *Cratoxylum sp.* | 530 | | |
| 15 | Leguminosae | *Crudia reticulata* Merr. | 932.5 | | |
| 9 | Lauraceae | *Cryptocaria sp.* | 610 | | NP |
| 8 | Leguminosae | *Cynometra inaequifolia* Knaap-v. M. | 960 | VU | |
| 10 | Burseraceae | *Dacryodes rostrata* Bl. | 660 | | |
| 9 | Lauraceae | *Dehassia sp.* | 740 | | NP |
| 15 | Urticaceae | *Dendrocnide elliptica* Chew | 619 | | |
| 15 | Leguminosae | *Dialium indum* L. | 980 | | |
| 15 | Dilleniaceae | *Dillenia excelsa* Jack | 865 | | |
| 15 | Sapindaceae | *Dimocarpus dentatus* | 870 | | NP |
| 15 | Sapindaceae | *Dimocarpus longan* Lour. | 870 | | NP |
| 15 | Sapindaceae | *Dimocarpus longan* Lour. | 870 | | NP |
| 8 | Ebenaceae | *Diospyros elliptifolia* Merr. | 940 | | NP |
| 8 | Ebenaceae | *Diospyros macrocarpa* L. | 1030 | | NP |
| 8 | Ebenaceae | *Diospyros muricata* L. | 1030 | | NP |
| 15 | Rubiaceae | *Diplospora sp.* | 619 | | |
| 5 | Dipterocarpaceae | *Dipterocarpus caudiferus* Merr. | 715 | | NP |
| 15 | Dracaenaceae | *Dracaena angustifolia* | 619 | | |
| 15 | Anacardiaceae | *Dracontomelon sp.* | 609 | | |
| 4 | Dipterocarpaceae | *Dryobalanops lanceolata* Burck | 810 | EN | NP |
| 15 | Euphorbiaceae | *Drypetes sp.* | 875 | | |
| 15 | Sonneratiaceae | *Duabanga moluccana* Bl. | 390 | | P |
| 15 | Bombacaceae | *Durio grandiflorus* Mast. | 625 | | |
| 15 | Meliaceae | *Dysoxylum sp.* | 710 | | |
| 15 | Elaeocarpaceae | *Elaeocarpus stipularis* Bl. | 565 | | |
| 9 | Lauraceae | *Endiandra rubescens* Miq. | 785 | | NP |
| 15 | Euphorbiaceae | *Endorspermum diadenum* Airy Shaw | 475 | | |
| 15 | Euphorbiaceae | *Endorspermum peltatum* Merr. | 380 | | |
| 8 | Annonaceae | *Enicosanthum sp.* | 659.5 | | |
| 9 | Myrtaceae | *Eugenia sp.* | 775 | | |
| 13 | Lauraceae | *Eusideroxylon zwageri* Teijs. & Binn. | 985 | VU | NP |
| 15 | Loganiaceae | *Fagraea volubilis* Wall. | 785 | | |
| 15 | Moraceae | *Ficus truebii* | 465 | | |
| 15 | Moraceae | *Ficus verigata* | 280 | | |
| 15 | Guttiferae | *Garcinia sp.* | 910 | | |
| 9 | Euphorbiaceae | *Glochidion rubrum* Bl. | 800 | | |
| 15 | Anacardiaceae | *Gluta wallichii* D. Hou | 725 | | |
| 15 | Sapindaceae | *Guioa pubescens* | 680 | | NP |
| 15 | Myristicaceae | *Gymnacranthera sp.* | 719 | | NP |
| 15 | Proteaceae | *Helicia sp.* | 647.5 | | |
| 9 | Sterculiaceae | *Heritiera elata* Ridley | 920 | | |
| 15 | Dipterocarpaceae | *Hopea beccariana* Burck | 745 | CR | NP |

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|---|---|---|---|---|---|
| 2 | Dipterocarpaceae | *Hopea nervosa* King | 750 | CR | NP |
| 15 | Flacourtiaceae | *Hydnocarpus borneensis* Sleumer | 820 | | NP |
| 15 | Flacourtiaceae | *Hydnocarpus kunstleri* | 820 | | NP |
| 15 | Flacourtiaceae | *Hydnocarpus polypetala* | 820 | | NP |
| 15 | Flacourtiaceae | *Hydnocarpus sumatrana* | 820 | | NP |
| 15 | Flacourtiaceae | *Hydnocarpus woodii* Merr. | 820 | | NP |
| 15 | Simaroubaceae | *Irvingia malayana* Oliv. ex Benn. | 1065 | | |
| 15 | Ixonanthaceae | *Ixonanthes sp.* | 825 | | |
| 15 | Tiliaceae | *Jarandersonia rinoreoides* | 619 | | NP |
| 15 | Guttiferae | *Kayea oblongifolia* | 619 | | |
| 15 | Apocynaceae | *Kibatalea arborea* | 619 | | |
| 15 | Myristicaceae | *Knema sp.* | 687.5 | | NP |
| 15 | Euphorbiaceae | *Koilodepas longifolium* Hook. | 990 | | |
| 15 | Euphorbiaceae | *Koilodepas pectinatum* | 990 | | |
| 15 | Meliaceae | *Lansium sp.* | 835 | | NP |
| 15 | Leeaceae | *Leea indica* Merr. | 510 | | |
| 9 | Fagaceae | *Lithocarpus sp.* | 807.5 | | |
| 9 | Lauraceae | *Litsea caulocarpa* | 562.5 | | NP |
| 9 | Lauraceae | *Litsea firma* Hk. | 575 | | NP |
| 15 | Celastraceae | *Lophopetalum javanicum* Zoll. | 545 | | |
| 15 | Rubiaceae | *Ludecia bornensis* | 667.5 | | |
| 15 | Euphorbiaceae | *Macaranga conifera* Muell. Arg. | 395 | | |
| 15 | Euphorbiaceae | *Macaranga gigantea* Muell. Arg. | 390 | | |
| 15 | Euphorbiaceae | *Macaranga hypoleuca* Muell. Arg. | 320 | | |
| 15 | Euphorbiaceae | *Macaranga pearsonii* Merr. | 355 | | |
| 9 | Sapotaceae | *Madhuca malaccensis* H.J. Lam | 760 | | NP |
| 15 | Magnoliaceae | *Magnolia candolii* H.Keng | 630 | | |
| 15 | Magnoliaceae | *Magnolia gigantea* | 607.5 | | |
| 15 | Magnoliaceae | *Magnolia gigantifolia* | 607.5 | | |
| 15 | Euphorbiaceae | *Mallotus muticus* Airy Shaw | 500 | | |
| 15 | Euphorbiaceae | *Mallotus penangensis* Muell. Arg. | 600 | | |
| 15 | Euphorbiaceae | *Mallotus phillippensis* Muell. Arg. | 705 | | |
| 15 | Euphorbiaceae | *Mallotus stipularis* Airy Shaw | 600 | | |
| 15 | Anacardiaceae | *Mangifera sp.* | 605 | | |
| 15 | Cornaceae | *Mastixia sp.* | 575 | | |
| 15 | Anacardiaceae | *Melanochylla sp.* | 680 | | |
| 15 | Rutaceae | *Melicope luna-akenda* T.G. Hartley | 420 | | P |
| 15 | Sabiaceae | *Meliosma pinnata* Maxim. | 385 | | NP |
| 15 | Sabiaceae | *Meliosma sumatrana* Walp. | 500 | | NP |
| 15 | Melastomataceae | *Memecylon sp.* | 960 | | |
| 15 | Tiliaceae | *Microcos crassifolia* Burret | 565 | | NP |
| 15 | Sapindaceae | *Mischocarpus sp.* | 930 | | NP |

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|---|---|---|---|---|---|
| 15 | Myristicaceae | *Myristica sp.* | 540 | | NP |
| 15 | Rubiaceae | *Nauclea subdita* Steud. | 590 | | P |
| 15 | Bombacaceae | *Neesia sp.* | 555 | | |
| 14 | Rubiaceae | *Neolamarckia cadamba* Bosser | 425 | | P |
| 15 | Rubiaceae | *Neonauclea artocarpoiedes* Merr. | 705 | | P |
| 15 | Rubiaceae | *Neonauclea gigantea* Merr. | 745 | | P |
| 15 | Rubiaceae | *Nephelium rambutan* | 850 | | NP |
| 15 | Olacaceae | *Ochanostachys amentacea* Mast | 910 | | |
| 11 | Datiscaceae | *Octomeles sumatrana* Miq. | 330 | | P |
| 9 | Sapotaceae | *Palaquium sp.* | 650 | | NP |
| 15 | Sapindaceae | *Paranephelium xestophyllum* Miq. | 1010 | | NP |
| 3 | Dipterocarpaceae | *Parashorea malaanonan* Merr. | 525 | CR | NP |
| 15 | Dipterocarpaceae | *Parashorea tomentella* Meijer | 397 | | NP |
| 15 | Sapotaceae | *Payena sp.* | 550 | | NP |
| 8 | Leguminosae | *Peltophorum racemosum* Merr. | 720 | | |
| 9 | Tiliaceae | *Pentace adenophora* Kost. | 640 | | NP |
| 9 | Tiliaceae | *Pentace laxiflora* Merr. | 640 | | NP |
| 15 | Rubiaceae | *Pleiocarpidia sandakanica* Brem. | 619 | | |
| 8 | Annonaceae | *Polyalthia obliqua* | 727.5 | | |
| 8 | Annonaceae | *Polyalthia sumatrana* Kurz | 727.5 | | |
| 15 | Sapindaceae | *Pometia pinnata* Forst. | 745 | | NP |
| 15 | Melastomataceae | *Pternandra coerulescens* Jack | 600 | | |
| 15 | Sterculiaceae | *Pterospermum elongatum* Korth | 517 | | |
| 15 | Euphorbiaceae | *Ptychopyxis kingii* Miq. | 650 | | |
| 15 | Flacourtiaceae | *Ryparosa sp.* | 690 | | NP |
| 8 | Annonaceae | *Sagerae lanceolata* Miq. | 730 | | |
| 8 | Meliaceae | *Sandoricum koetjape* Merr. | 420 | | NP |
| 10 | Burseraceae | *Santiria tomentosa* Bl. | 650 | | |
| 15 | Leguminosae | *Saraca declinata* Miq. | 600 | | |
| 15 | Sterculiaceae | *Scaphium sp.* | 657.5 | | |
| 15 | Dipterocarpaceae | *Shorea agamii* Ashton | 665 | EN | NP |
| 7 | Dipterocarpaceae | *Shorea atrinervosa* Sym. | 945 | | NP |
| 15 | Dipterocarpaceae | *Shorea faguetiana* Heim | 550 | EN | NP |
| 2 | Dipterocarpaceae | *Shorea falciferoides* Foxw. | 892.5 | | NP |
| 2 | Dipterocarpaceae | *Shorea fallax* Meijer | 625 | | NP |
| 6 | Dipterocarpaceae | *Shorea gibbosa* Brandis | 605 | | NP |
| 1 | Dipterocarpaceae | *Shorea johorensis* Foxw. | 507.5 | CR | NP |
| 2 | Dipterocarpaceae | *Shorea leprosula* Miq. | 555 | EN | NP |
| 15 | Dipterocarpaceae | *Shorea leptoderma* Meijer | 956.3 | CR | NP |
| 15 | Dipterocarpaceae | *Shorea macroptera* Dyer | 480 | | NP |
| 2 | Dipterocarpaceae | *Shorea parvifolia* Dyer | 562.5 | | NP |
| 15 | Dipterocarpaceae | *Shorea parvistipulata* Heim | 312 | | NP |

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|---|---|---|---|---|---|
| 2 | Dipterocarpaceae | *Shorea pauciflora* King | 662.5 | EN | NP |
| 15 | Dipterocarpaceae | *Shorea superba* Sym. | 895 | | NP |
| 9 | Leguminosae | *Sindora sp.* | 675 | | |
| 15 | Euphorbiaceae | *Spathiostemon javensis* | 619 | | |
| 15 | Icacinaceae | *Stemonurus scorpioides* Becc. | 615 | | |
| 9 | Leguminosae | *Sympetalandra borneensis* Stapf | 790 | | |
| 15 | Symplocaceae | *Symplocos fasciculata* Zoll. | 430 | | |
| 15 | Verbenaceae | *Teijsmanniodendron bogoriense* Koord. | 447.5 | | |
| 15 | Verbenaceae | *Teijsmanniodendron pteropodum* Bakh. | 465 | | |
| 15 | Combretaceae | *Terminalia citrina* Roxb. | 827.5 | | |
| 15 | Rubiaceae | *Urophyllum sp.* | 619 | | |
| 15 | Dipterocarpaceae | *Vatica albiramis* van Slooten | 673 | | NP |
| 3 | Dipterocarpaceae | *Vatica dulitensis* Sym. | 820 | | NP |
| 15 | Verbenaceae | *Vitex sp.* | 675 | | |
| 15 | Meliaceae | *Walsura pinnata* Hassk. | 1005 | | NP |
| 15 | Polygalaceae | *Xanthophyllum flavecescens* | 805 | | |
| 15 | Rhamnaceae | *Zizyphus angustifolius* Miq. | 807.5 | | |

Table S3: Comparison of estimated above-ground tree biomass for logged (SBE: Sabah Biodiversity Experiment) and unlogged (DV: Danum Valley) forest. Per transect: Sum of all 4 transects (each 0.25 ha) ± 95% CI. 1st, 2nd, 3rd, 4th transect: Each transect (250 m x 10 m) multiplied by 4 to get an estimated biomass for 1 ha forest area.

| | **Per transect** | **1st** | **2nd** | **3rd** | **4th** |
|---|---|---|---|---|---|
| **SBE** | **272.1 ± 46.5** | **275.6** | **277.0** | **232.6** | **303.1** |
| **DV** | **468.6 ± 207** | **466.7** | **503.7** | **295.5** | **608.5** |

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# 6 Chapter Three

## 6.1 Reduced Soil Respiration in Gaps in Logged Lowland Dipterocarp Forest

*(with R. Lim, B. Burla, R.C. Ong, M. Scherer-Lorenzen, A. Hector. 2009 Forest Ecology and Management,* **258***, 2007-2012)*

## 6.2 Abstract

We studied the effects of forest composition and structure, and related biotic and abiotic factors on soil respiration rates in a tropical logged forest in Malaysian Borneo. Forest stands were classified into gap, pioneer, non-pioneer and mixed (pioneer, non-pioneer and unclassified trees) based on the species composition of trees >10 cm diameter breast height. Soil respiration rates did not differ significantly between non-gap sites (1290 ± 210 mg $CO_2$ $m^{-2}$ $h^{-1}$) but were double those in gap sites (640 ± 130 mg $CO_2$ $m^{-2}$ $h^{-1}$). Post-hoc analyses found that an increase in soil temperature and a decrease in litterfall and fine root biomass explained 72% of the difference between gap and non-gap sites. The significant decrease of soil respiration rates in gaps, irrespective of day or night time, suggests that autotrophic respiration may be an important contributor to total soil respiration in logged forests. We conclude that biosphere-atmosphere carbon exchange models in tropical systems should incorporate gap frequency and that future research in tropical forest should emphasize the contribution of autotrophic respiration to total soil respiration.

**Keywords**

tropics, Borneo, logged forest, carbon cycle, gap dynamics, soil ecology

## 6.3 Introduction

Forest ecosystems contain an estimated 638 Gt (60%) of the carbon stored in terrestrial ecosystems and could potentially absorb about 10% of global carbon emissions projected for the first half of this century (Streck et al., 2008). At the same time, 13 million hectares of tropical deforestation per year contribute to 20% of global carbon emissions (Canadell et al., 2008). The increasing importance of the remaining tropical forests for climate change mitigation is therefore a topic of broad interest (Chazdon, 2008, Putz et al., 2008). Intact forest cover of the Indo-Malaya region (including South Asia, Southeast Asia and Papua New Guinea) was less than 40 percent of the original area by 2000 (Wright and Muller-Landau, 2006).

At a regional scale, logged forests cover more than 85 percent of the remaining forest area in the state of Sabah (Malaysian Borneo) where the present study was undertaken (Sabah Forestry Department, unpubl. data). In the light of these current trends it is crucial to better understand biogeochemical cycling in tropical forest ecosystems and in particular in logged forest over the long term (Sayer et al., 2007). Compared to a primary forest the altered vegetation composition and structure of a logged forest leads to changes in microclimatic conditions. For example logged forests are known to be more susceptible to fires than unlogged forests, mainly due to drying of the forest floor (Collins et al., 2004). Further, the absence of large trees and the resulting lower frequency and size of canopy gaps have been shown to disturb succession in regenerating forests of peninsular Malaysia (Numata et al., 2006). However, to date little is known about how changes in forest structure and composition influence biogeochemical cycles and in particular total $CO_2$ efflux at the soil surface, known as soil respiration (Ostertag et al., 2008).

Soil respiration is a substrate driven process consisting of four main sources of carbon compounds, namely carbon from litter, soil organic matter (SOM), roots, and root exudation processes (Berg and McClaugherty, 2003). Based on the source of the carbon, total soil respiration can be divided into heterotrophic respiration by microbes (mainly litter and SOM) plus autotrophic respiration by roots, mycorrhiza and the rhizosphere (Hansen, 2001). Differences among tree species in litter quality, quantity, timing of litter input and respiratory activities in roots have been shown recently (Bjornlund and Christensen, 2005, Hattenschwiler and Gasser, 2005, Scherer-Lorenzen et al., 2007). Studies from boreal systems show that litter decomposition and the turnover of soil organic matter (SOM) are affected by tree species composition and diversity, and that forest composition may alter soil respiration rates (Borken and Beese, 2005). Further factors that were shown to alter changes of heterotrophic and autotrophic respiration in forest ecosystems in either gaps or under closed canopy include soil temperature and soil water content (Davidson et al., 2000, Ritter et al., 2005), precipitation (Raich and Schlesinger, 1992), light interception

(Zhang and Zak, 1995), root biomass (Soe and Buchmann, 2005) and nutrient availability (Cleveland and Townsend, 2006). (Ohashi et al., 2008) showed that spatial variation in soil respiration may be higher than either seasonal or diurnal variation in tropical forests of South-East Asia. Based on these findings the principal objective of our work was to determine if changes in forest composition and structure could explain some of the spatial patterns of soil respiration in logged forests. We were interested in the following research questions:

Do soil respiration rates change depending on forest composition?

Do soil respiration rates differ in gap sites compared to non-gap sites?

Do soil respiration rates differ between day- and night time?

Which abiotic and biotic factors explain the changes found?

## 6.4 Material and Methods

### 6.4.1 Site description

Our study area (N05°05'20" E117°38'32", 102 m a.s.l.) was located in the eastern part of the province of Malaysian Sabah in northern Borneo. The region is aseasonal with an annual rainfall of ca. 3000 mm during the measurement period (2004-2008) (Chapter 1). Cumulative daily rainfall was measured at 07:00 am using a standard rain gauge (Novalynx, USA). The forest belongs to a one million hectare concession area of the Sabah Foundation and is classified as secondary lowland mixed dipterocarp production forest. It is situated 65 km north to the Danum Valley Field Centre, which forms part of the Danum Valley Conservation Area (Marsh and Greer, 1992). The study was set up within a large scale forest rehabilitation project called the Sabah Biodiversity Experiment which covers an area of 500 hectares of logged forest in the Malua Forest Reserve. The experiment aims to study the importance of tree species diversity, composition and life history traits for providing fundamental ecosystem services, such as carbon sequestration

(Scherer-Lorenzen et al., 2005). The vegetation composition of a logged forest depends on its previous successional stage in primary condition, damage caused by the logging operation and the time allowed for regeneration (Bischoff et al., 2005). In our case the forest was logged by conventional methods about 30 years ago (early 1980s), whereby only trees > 45 cm diameter breast height (DBH) were harvested. Due to heavy disturbance of the understorey seedling bank the forest developed thereafter into a mixed stand of sites that were dominated by pioneer trees and other, less severely damaged sites that consisted of non-pioneer trees (Turner, 2001). Overall, the basal area for trees > 10 cm diameter breast height (DBH) was 25.0 ± 0.9 (SEM) $m^2$ $ha^{-1}$ and tree density was estimated as 417 per hectare (Saner, unpubl. data). Litterfall (11.7 ± 0.3 t $ha^{-1}$ $yr^{-1}$) measured over one year was comparable to close-by primary forest (Burghouts et al., 1992) and at the upper end of reported estimates from old-growth Amazonian forests (5.2 - 12.5 t $ha^{-1}$ $yr^{-1}$) (Chave et al., 2009). The soil was classified as orthic acrisol, which is acidic (pH>5), highly weathered with poor nutrient availability (81 % base saturation) and a low organic carbon content (topsoil: 1.2 %, 1m depth: 0.6%) (Saner, unpubl. data). Bedrock consisted of a mixture of mudstone and sandstone areas with miscellaneous rocks (Forestry Department Sabah 2006, unpubl. data).

### 6.4.2 Forest structure and composition

Seven transect lines (750 x 10 m) were established 100 m apart from each other and each line was sub-divided into seventy-five 10 x 10 m sites. Local taxonomic experts measured and identified all trees >10 cm DBH along the transect lines to species level. The sites were then classified into gap, pioneer, mixed and non-pioneer based on the tree species composition. Gap sites were defined as openings in the canopy layer (5 to 20 % of visible sky) as a result of tree- or branchfall. Light interception, defined here as the percentage of canopy openness at each site was determined at the start of the experiment using a Spherical Densiometer Model A (Lemmon, USA). They were selected by visual examination, based on

experience of estimating canopy openness using densiometers, hemispherical photographs and measurements of photosynthetic active radiation (PAR) in other studies in Danum Valley (Whitmore et al., 1993). Pioneer sites were defined as areas covered by highly light demanding species. We identified *Duabanga moluccana* Bl. (Sonneratiacea), *Macaranga sp.* Muell. Arg. (Euphorbiaceae), *Melicope luna-akenda* T.G. Hartley (Rutaceae), *Octomeles sumatrana* Miq. (Datiscaceae) and *Ludecia bornensis, Nauclea subdita* Steud., *Neolamarckia cadamba* Bosser, *Neonauclea sp.* Merr. (Rubiaceae) as pioneer trees. Non-pioneer sites were identified as those that had species which were slow growing with a high wood density, in particular from the families of the Dipteroarpaceae, Ebenaceae, Flacourtiaceae, Lauraceae, Meliaceae, Myristicaceae, Sabiaceae, Sapindaceae, Sapotaceae and Tiliaceae. Non-pioneer trees were expected to invest more photoassimilates into defense mechansims which would result in leaf litter that consisted of higher concentrations in secondary compounds, such as polyphenols, condensed tannins or terpenoids (Grime et al., 1996, Whitmore, 1998). These were shown to be relatively resistant to microbial decay and therefore may alter soil respiration rates (Ostertag et al., 2008), but see (Kurokawa and Nakashizuka, 2008). Mixed sites consisted of trees belonging to both pioneers and non-pioneers (as well as trees that could not be distinguished into either one of the two classifications; unknown) (Table S2).

### 6.4.3 Experimental set-up

Ten gaps were randomly chosen along the transect lines. Within 100 m of each gap site we selected a pioneer, a mixed and a non-pioneer site for direct comparison. The four sites (gap, pioneer, mixed and non-pioneer) were therefore replicated ten times each, resulting in forty measured sites which represented the forest classifications. We excluded riverbeds and skid trails due to possible effects of soil compaction on soil respiration rates. One single PVC collar (7 cm x 21 cm diameter) was inserted 2 cm into the soil at each of the forty selected sites two weeks prior to the start of the experiment.

### 6.4.4 Measuring soil respiration

The soil respiration chamber was self-made following Pumpanen et al. (2004). It consisted of an airtight, non-through-flow PVC cylinder (30 cm x 21 cm diameter) with a small ventilator connected to a 12 V battery (Uusima, 2003). Soil respiration measurements were taken at all collars between May to June 2007 using an Infrared Gas Analyzer CARBOCAP GMP343 (Vaisala, Finland). During chamber placement we opened a blow-off valve to control for overpressure inside the chamber. Day time measurements were taken once per collar on seven days (n = 280) between 08:00 am and noon. For logistic reasons we were unable to record the diurnal changes reported in previous studies (Ohashi et al., 2008). Night time measurements were taken once per collar on two days (n = 80) between 08:00 pm and 04:00 am. Soil respiration measurements were taken over five minutes per collar, whereby the first two minutes were disregarded to avoid disturbance effects caused by chamber placement. Soil respiration rates were calculated from the rate of $CO_2$ efflux inside the chamber over the remaining three minutes interval. Even though we measured over a relatively short time span, treatment effects between gap and non-gap sites were clear and it is relative changes in percentages that are the focus of our study.

### 6.4.5 Measuring covariables

All soil and air measurements were done in combination with the soil respiration measurements. Soil temperature and soil moisture were measured at 5 cm depth with a WET Sensor (Delta-T, UK). Air relative humidity (%) and air temperature ($^oC$) were measured with a HMP75 probe (Vaisala, Finland). At all forty selected sites we established 1 $m^2$ quadrats to collect standing litter and root biomass at the start of the experiment to avoid effects of site disturbance. Soil cores (100 $cm^3$) were taken vertically from the top mineral soil layer (0-5 cm) of each quadrat using standard soil corers (Eijkelkamp, Netherlands). Root biomass was extracted by washing the soil cores over a 210 µm sieve (Retsch, Germany). Litterfall

traps (1 $m^2$) were established next to the selected quadrats at 1.3 m height, using fine (1 x 1 mm) meshed plastic net. Litter was collected twice during the measurement period. All collected root biomass and litter samples were dried (60°C for 48 h) to constant weight before weighing. Litter was further separated into leaves, twigs (typically < 1 cm in diameter) and reproductive organs (flowers and fruits). One litterfall measurement was discarded from the analysis because of a freshly fallen climber fruit that biased the litterfall rate of a non-pioneer site (> 7 g $day^{-1}$).

### 6.4.6 Data analysis

We analyzed differences in continuous response variables with a mixed effects ANOVA using restricted maximum likelihood with the *lmer* function from the *lme4* package (Bates et al., 2008) for R 2.6.2 (R Development Core Team, 2008). The model was fitted to the data using an identity link function and specifying that the variance should increase as the square of the mean (Gamma error distribution). The lmer function currently does not provide p values for the approximate F-tests for fixed effects. Instead we performed pre-planned contrasts of the three non-gap sites (forest composition: pioneer, mixed, non-pioneer) relative to the gap sites using t-tests. We present point estimates of the means with their standard errors (SEM) from the fitted model. We included time when analysing the importance of forest composition and structure on soil respiration rates. Spatial and temporal replicates were included as random terms into the model. Forest classification (gap, pioneer, mixed and non-pioneer) and measurement time (day, night) were included as fixed effects.

For subsequent analysis of the importance of measured covariables the data set had to be collapsed as values of all covariates were not taken at all time points. Therefore, we used a linear analysis of covariance (ANCOVA). Rather than averaging the day and night measurements that had unequal replication, the two night time measurements were omitted and we used day respiration rates only for further analysis.

Covariables were chosen based on their importance from literature and if not highly correlated with one another. Selected covariables were then fitted individually into the model to test for their potential effect on day soil respiration rates. Data were checked for normal distribution and heterogeneity of residuals. We also examined a small number of multiple regressions using variables selected a priori for testing.

## 6.5 Results

### 6.5.1 The importance of forest composition and structure

Soil respiration rates were highly variable over time and space (78% of the summed variance components from the mixed-effects model). However, there was no particular positive or negative trend over time. Soil respiration rates in gap sites (640 ± 130 mg $CO_2$ $m^{-2} h^{-1}$; n = 10) were significantly lower than in pioneer sites (1260 ± 190; t = 4.6, p<0.001), mixed sites (1260 ± 200; t = 4.5, p<0.001) and non-pioneer sites (1360 ± 210; t = 5.0, p<0.001), suggesting that forest structure is an important factor determining spatial changes in soil respiration. The average of all non-gap sites (1290 ± 210 mg $CO_2$ $m^{-2} h^{-1}$) was approximately double gap sites. Differences between non-gap sites (pioneer, mixed and non-pioneer) were not significant, indicating that forest composition only had a minor influence on spatial patterns of soil respiration rates (Table 4).

Table 4 Mean (± SEM; calculated for each group individually) for all measured variables at gap and non-gap sites (pioneer, mixed, non-pioneer). Measurements that were taken together with soil respiration rates are reported separately for day (n = 7) and night (n = 2) time measures.

| | | Gap | | Pioneer | | Mix | | Non-Pioneer | |
|---|---|---|---|---|---|---|---|---|---|
| | | Day | Night | Day | Night | Day | Night | Day | Night |
| Soil respiration | [mg $CO_2$ $m^{-2}$ $h^{-1}$] | 733 ± 163 | 553 ± 133 | 1399 ± 216 | 1118 ± 256 | 1380 ± 223 | 1134 ± 159 | 1472 ± 187 | 1257 ± 193 |
| Soil temperature | [°C] | 25.9 ± 0.3 | 26.2 ± 0.1 | 25.5 ± 0.2 | 25.9 ± 0.1 | 25.2 ± 0.1 | 25.6 ± 0.1 | 25.4 ± 0.1 | 25.7 ± 0.1 |
| Air temperature | [°C] | 26.4 ± 0.3 | 26.5 ± 0.1 | 26 ± 0.2 | 26.1 ± 0.2 | 25.8 ± 0.1 | 26 ± 0.1 | 25.9 ± 0.1 | 25.7 ± 0.1 |
| Soil water content | [%] | 37.5 ± 2.1 | 35.5 ± 2.4 | 35.3 ± 2.2 | 34 ± 2.7 | 30.4 ± 2.3 | 29.9 ± 2.5 | 29.9 ± 2.2 | 28.8 ± 2.2 |
| Relative humidity | [%] | 91 ± 0.3 | 93.9 ± 0.3 | 90 ± 0.6 | 93 ± 0.5 | 90.2 ± 0.6 | 93.5 ± 0.3 | 90.4 ± 0.8 | 94 ± 0.3 |
| Light interception | [%] | 12.2 ± 1.6 | | 3.6 ± 1.1 | | 3.1 ± 1.1 | | 3.2 ± 0.8 | |
| Standing litter | [g $m^{-2}$] | 153 ± 27 | | 135 ± 14 | | 178 ± 30 | | 168 ± 20 | |
| Root biomass (> 5cm) | [g $m^{-2}$] | 120 ± 13 | | 156 ± 35 | | 251 ± 56 | | 218 ± 26 | |
| Litterfall | [g $m^{-2}$ $d^{-1}$] | 1.8 ± 0.3 | | 2.4 ± 0.3 | | 2.7 ± 0.4 | | 2.0 ± 0.2 | |
| Basal area | [$m^2$ $ha^{-1}$] | 9.5 ± 3.2 | | 24.4 ± 3.0 | | 31.5 ± 5.8 | | 24.4 ± 3.4 | |

### 6.5.2 Comparing day and night soil respiration rates

The effect of forest structure and composition on soil respiration rates was irrespective of the measurement period (day/night) (test of interaction: t = 0.3, p = 0.36). On average, measurements at night were 20% lower than at daytime (t = 2.2, p = 0.04) (Fig.13). Relative changes between day and night measurements were highest in gap sites (25%) and were lower for pioneer, mixed and non-pioneer sites (20%, 18% and 15% respectively). Interestingly, environmental covariables did not show daily fluctuations, except for a slight increase in relative air humidity during the night (Table 4).

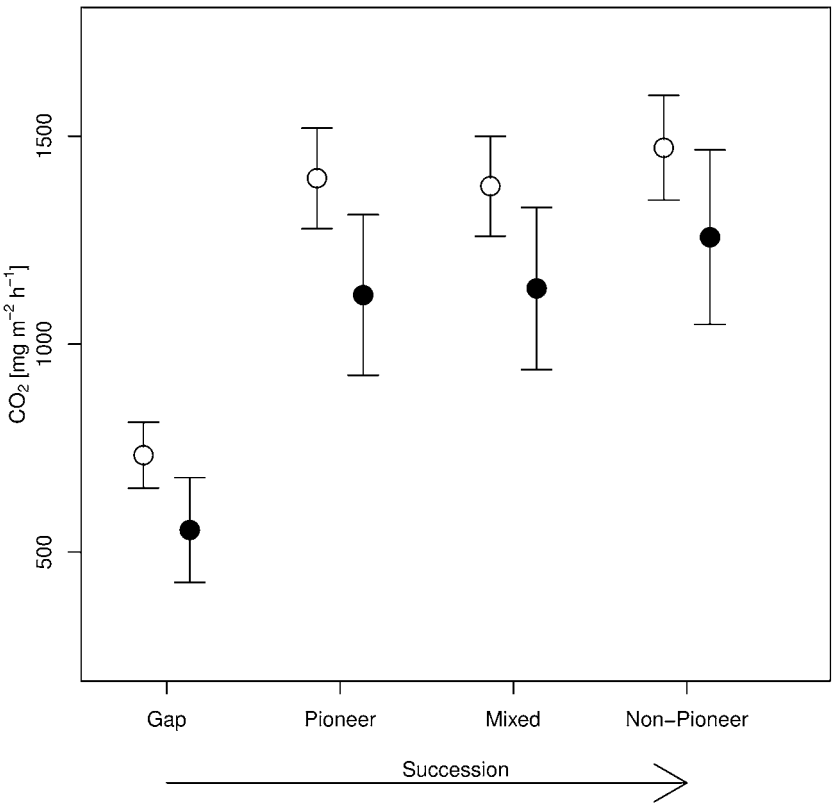


Figure 13 Soil respiration rates ($CO_2$ [mg $m^{-2}$ $h^{-1}$] (mean ± SEM)) along the successional gradient, ranging from gap sites to pioneer, mixed and non-pioneer sites. White circles indicate day soil respiration rates, black circles indicate night soil respiration rates.

### 6.5.3 The importance of selected abiotic and biotic factors

For subsequent post-hoc analysis all non-gap sites (pioneer, mixed and non-pioneer) were pooled to consider the gap versus non-gap site contrast only. Covariables such as litterfall and root biomass were measured only twice or once, respectively during the period of soil respiration measurements. Therefore arithmetic means over time for all other covariables were used for the subsequent analysis of covariance (ANCOVA) too. The data set was unbalanced and the sequential ANOVA order-dependent, therefore selected covariables were fitted both first and last in the model to bracket their effect on total variation (%) and how much they reduced the effect of the gap versus non-gap site contrast. Except for standing litter all covariables differed significantly between gap and non-gap sites: Soil temperature ($t = 2.4$, $p < 0.05$), soil water content ($t = 2.2$, $p < 0.05$), litterfall ($t = 2.7$, $p < 0.05$), fine root biomass ($t = 2.1$, $p = < 0.05$), basal area ($t = 3.7$, $p < 0.001$), standing litter ($t = 0.3$, $p = 0.79$). To reduce colinearity only covariables that were not highly correlated with each other ($r < 0.27$) were considered for analysis (Table 5a). Overall, an increase in soil temperature and a decrease in litterfall and root biomass explained 72% of the difference between gap and non-gap sites (Fig.14). Soil temperature was the single most important covariable, explaining 14-16% (fitted first and last into the model) of the total variation and reducing the effect of the gap versus non-gap sites contrast by 54% (Test of soil temperature fitted in first place; $F_{1,25} = 10.0$, $p < 0.01$). Litterfall explained 7-9% of the total variation and reduced the contrast effect by 44% ($F_{1,25} = 7.2$, $p < 0.05$). Contrary to our expectations, fine root biomass explained <1% of the total variation (Table 5a). Neither soil water content nor standing litter did have a substantial influence on the total variation. Further, substituting litterfall and fine root biomass by tree basal area did not result in a better explanation of the gap versus non-gap sites contrast (Table 5b).

Table 5 Fitting the terms first and last in the ANCOVA model. F-value, percentage of total sum of squares and t-values are shown. Replication: block that consists of all four sites (n = 10); gap, pioneer, mixed, non-pioneer (n = 40). Sites: Gap versus non-gap sites contrast. (a): Final model, (b): Fitting Basal Area instead of litterfall and fine root biomass.

| (a) | Fitted in first place | | Fitted in last place | | |
|---|---|---|---|---|---|
| | F | % SS | F | % SS | t |
| Replication | 2.0 | 28.0 | – | – | – |
| Soil temperature | 10.0 | 15.9 | 9.0 | 14.3 | 1.8 |
| Litterfall | 7.2 | 11.5 | 5.7 | 9.1 | 0.9 |
| Fine root biomass | < 0.1 | < 1 | 0.4 | < 1 | 1.4 |
| Contrast | – | – | 3.9 | 6.2 | 2.0 |

| (b) | Fitted in first place | | Fitted in last place | | |
|---|---|---|---|---|---|
| | F | % SS | F | % SS | t |
| Replication | 1.9 | 26.9 | – | – | – |
| Soil temperature | 10.3 | 16.1 | 9.1 | 14.2 | 1.8 |
| Basal area | 1.3 | 2.0 | 0.1 | < 1 | 1.6 |
| Sites | – | – | 9.5 | 14.8 | 3.1 |

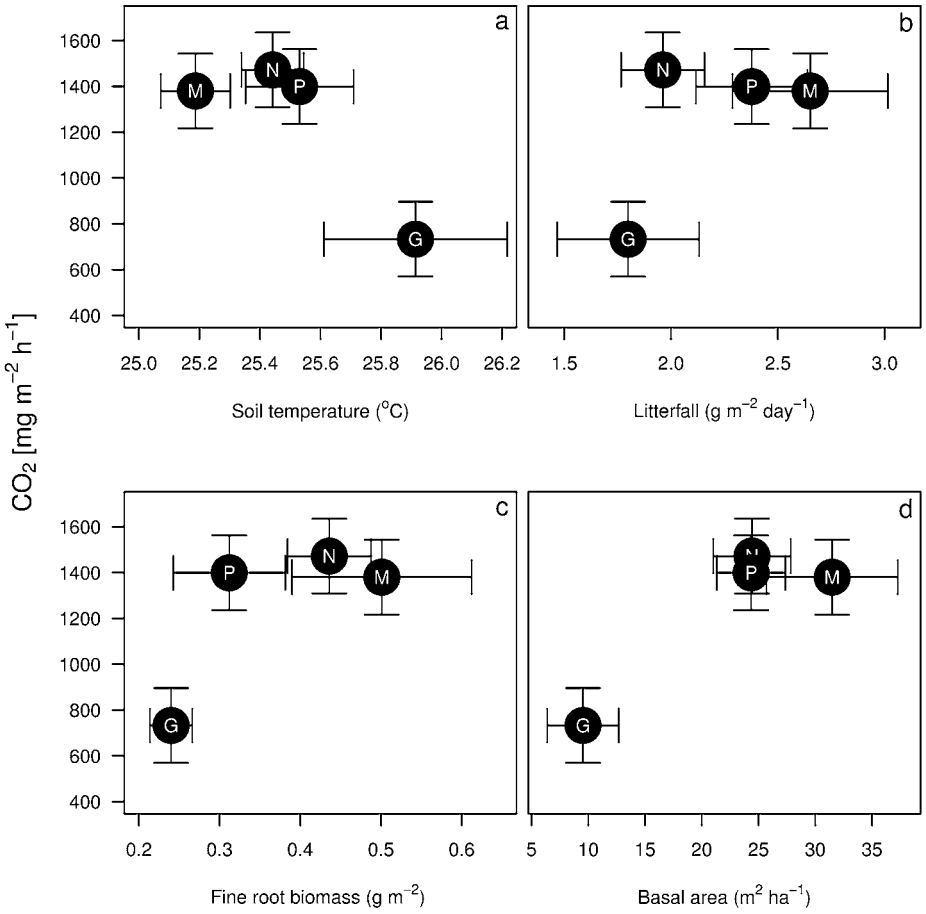


Figure 14 Effects of the selected explanatory variables on day time measurements of soil respiration rates ($CO_2$ [mg $m^{-2}$ $h^{-1}$] (mean ± SEM)); (a) Soil temperature, (b) Litterfall, (c) Root biomass, (d) Basal area. G: gap, P: pioneer, M: mixed, N: non-pioneer sites.

## 6.6 Discussion

Our results showed that forest composition did not affect soil respiration rates: all non-gap sites (pioneer, mixed and non-pioneer) showed similar soil respiration rates, regardless of the vegetation type. In contrast, gap sites had significantly lower soil respiration rates. This result is in accordance with findings from secondary forests of peninsular Malaysia (Adachi et al., 2006) where they found a lower gap site C efflux (mean ± SEM; 576 ± 93 mg $CO_2$ $m^{-2}$ $h^{-1}$) compared to the sub-canopy sites (838 ± 36) (our test based on reported SEM and sample size: t = 2.62, p = 0.02). Adachi et al. (2006) explained spatial variation in soil respiration in tropical primary and secondary forests of peninsular Malaysia with a higher soil mois-

ture and a lower fine root biomass in gaps compared to the sub-canopy. In gap sites we measured higher soil temperature, soil water content and light interception (Poulson and Platt, 1996, Scharenbroch and Bockheim, 2007) but lower fine litterfall rate (Bauhus and Bartsch, 1995), fine root biomass (Cuevas and Medina, 1988, Denslow et al., 1998) and basal area compared to non-gap sites (Table 4). These findings suggest that higher light interception led to a temperature increase on the soil surface, however the difference is relatively small across sites (<1°C change between gap and non-gap sites for day time measurements). In addition, fewer trees in gap sites caused a higher soil water content due to lower water absorption (although soil in gap sites is not necessarily wetter than in understorey areas (Poorter, 2005) and simulation studies indicate a complex interaction between soil drying, gap size, litter level and the presence or absence of roots from surrounding vegetation (Marthews et al., 2008). Measured covariables explained approximately two third of the difference between gap and non-gap sites. Other factors such as nitrogen concentration or soil organic matter (SOM), might have explained further variation, although these were found to be important shortly after gap formation rather than in established gaps (Denslow et al., 1998). In addition, studies on artificial gaps in Maracá Island, Brazil found that neither soil microbial biomass, soil respiration, nor nitrogen mineralization were enhanced in the forest compared to open areas (Luizao et al., 1998). Studies from subtropical China found that gap size was a proximate factor of substrate-induced respiration, with the ultimate factor being soil moisture (Zhang and Zak, 1995). They measured gaps between five to forty meters in diameter, where small natural disturbances (gap size of 15 m in diameter) did not affect overall nutrient cycling rates, whereas large scale disturbances inhibited nutrient release. They reported a decrease in litter decay from 57 to 44 % from closed forest to gap sites that correlated with a decrease in soil moisture from 19.2 to 11.4 % in the large gaps. Based on these findings they suggested that abiotic conditions such as soil temperature and soil water content correlated positively with soil respiration if gaps and sub-canopy sites were compared. In contrast to such previous findings we

could determine soil temperature, but not soil water content to be relevant for differences in soil respiration rates between gap and non-gap sites. However, small absolute differences in soil temperature suggest that biotic factors (e.g. litterfall and root biomass) may be relevant to explain observed changes in soil respiration rates between gap and non-gap sites. The lack of big trees in the gap sites resulted in a lower litterfall rate and lower fine root biomass (although decreased levels of fine root biomass could not explain altered soil respiration rates). A recent study by Katayama et al. (2009) reported the first evidence that soil respiration rates were positively related to mean diameter at breast height of trees within 6 m of the measurement point. Even though we could not find evidence for a relation between tree basal area and soil respiration rates, our results indirectly support their findings that tree presence increases soil respiration. Whether gap specific processes or the mere presence of large trees are more relevant for spatial variation in tropical forests would be interesting to test in the future.

Total soil respiration in gaps compared to non-gap sites is likely to depend on different relative shares of autotrophic and heterotrophic respiration. We found a significant decrease in soil respiration rates from day to night measures in both, gap and non-gap sites. Higher concentrations of photosynthetic assimilates in the roots and a resulting increase in autotrophic respiration during the day may partly explain the difference found. However, this assumption can be challenged since environmental variables such as light irradiance, air temperature, soil water content and air humidity are likely to change during the course of the day. In particular in gaps this may alter the contribution of heterotrophic respiration to total soil respiration rates. In our study, daily soil respiration fluctuations were decoupled from changes in environmental covariables and in particular from soil temperature (Table 4), similar to the findings of studies from Yucatan Peninsula in Mexico (Vargas and Allen, 2008) but in contrast to findings from the Amazonas, Brazil (Sotta et al., 2004). Such decoupled effects suggest that day and night time soil respiration should be measured separately when quantifying total ecosystem respiration (Katayama et al., 2009). Further,

the day to night time difference in soil respiration rates between gap and non-gap sites could be simply due to the physical presence of a canopy, enhancing carbon storage during the night (Iwata et al., 2005). Studies of gap dynamics have focused on changes in heterotrophic respiration. However the contribution of autotrophic respiration, in particular mycorrhizal respiration, could be an important reason for the decrease of total soil respiration rates in forest gaps. Studies from temperate beech forest gaps showed that $CO_2$ fluxes were 40% lower compared to a mature stand which were explained based on differences in root respiration (Brumme, 1995). Girdling experiments or isotopic approaches (Hanson et al., 2000) would be necessary to draw further conclusions about the relative shares of the different components on total soil respiration rates in tropical lowland dipterocarp forests.

## 6.7 Conclusion

Forest structure, in particular the frequency of gaps, is relevant when quantifying soil respiration in logged forest. In addition, relative differences in soil respiration rates between day- and night time may be important to consider when quantifying total ecosystem respiration. These findings are of particular interest for implementing biosphere-atmosphere carbon exchange models in tropical systems. We emphasize that future research in tropical forest should focus on the contribution of autotrophic respiration to total soil respiration.

## 6.8 Acknowledgements

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# 7 Chapter Four

## 7.1 Carbohydrate Allocation to Growth and Reserves by Dipterocarp Seedlings

*(with C. Philipson, S. Peters, F. Keller, L. Bigler, L. Turnbull, A. Hector, manuscript)*

## 7.2 Abstract

We experimentally forced seedlings of the Dipterocarpaceae family into altered carbon balance by manipulating light environments in a shadehouse experiment to simulate gap formation or closure. Simulation of canopy gap dynamics should reveal if seedlings allocate photosynthate into current growth or non-structural carbohydrate reserves (starch and soluble sugars). Growth in mass was modelled with two general approaches: (1) a linear mixed effects model of initial size-corrected average RGR (where size correction is done by including initial size as a covariate in the mixed effects model), and (2) a non-linear mixed effects model analysing growth as a power function. Seedling adaptation to a gap opening indicated a trade-off between allocation of carbohydrates to growth or reserves in five out of six dipterocarp species. A previously unknown polyol (Iditol) was common to all six species and its share to non-structural carbohydrates was 3 – 47% depending on species and light environment. Plausible roles of polyols for stress tolerance in tropical trees are further discussed.

**Keywords**

Dipterocarpaceae, shade tolerance, carbon, growth, polyols, Iditol

## 7.3 Introduction

Seedling growth in natural forest gaps is determined by ecological adaptation to given resources and the effect of chance (Hubbell et al., 1999, Brokaw and Busing, 2000, Hubbell, 2005). Light is a key resource for the juvenile stage of a tree and is highly variable during the process of canopy gap dynamics (Canham, 1989, Denslow et al., 1998, Poorter, 2005, Marthews et al., 2008). Here we define canopy gap dynamics as openings or closures in the forest stand caused by either tree- or branchfall (Whitmore, 1989, Parsons et al., 1994). The relevance of canopy gap dynamics for altered light environments led to many explanations for mechansims of tree species coexistence in forest gaps (Platt and Strong, 1989). For example, the

gap-size niche partitioning hypothesis predicts that tree species are adapted to particular microclimatic conditions, therefore changes in gap size are proposed to drive tree species coexistence (Connell, 1978, Hartshorn, 1978, Denslow, 1980). Others perceived gradual changes in the gap environment as the cause for crossovers in seedling growth and argue that species are specialized on particular light levels which may explain tree diversity (Givnish, 1988, Latham, 1992, Sack and Grubb, 2001). Those concepts were tested independently in tropical studies and challenged for their over-simplicity (Brokaw and Scheiner, 1989, Raich and Christensen, 1989, Brown and Whitmore, 1992, Barker et al., 1997, Agyeman et al., 1999, Brown et al., 1999, Kitajima and Bolker, 2003, Sack and Grubb, 2003, Baraloto et al., 2005). Yet another concept—that was the basis for this study—highlights the proposed life history trade-off between growth in light conditions of canopy gaps versus survival in the dark forest understorey (Hubbell and Foster, 1992, Kitajima, 1994, Kobe et al., 1995, Poorter, 1999). Sudden increases or decreases in light may force a seedling to selectively allocate resources into structural tissue (e.g. leaves, stem, branches and roots) for current growth or into carbohydrate reserves for prolonged survival (Kobe, 1997, Canham et al., 1999). If seedlings exposed to sudden changes in the light environment allocate carbohydrates into either current growth or reserves for later survival this may reveal how an unpredictable resource - such as light in a tropical forest - can promote coexistence by allowing species to partition forest light environments (Myers and Kitajima, 2007, Poorter and Kitajima, 2007). The processes that drive tree species coexistence in tropical forests are manifold (Whitfield, 2002) and have been studied extensively at the seedling stage (Augspurger, 1984, Moad, 1992, Zipperlen, 1997, Bloor, 2003, Baltzer and Thomas, 2007, Baraloto and Forget, 2007). However few have tested how seedlings respond to sudden changes in light as may occur during gap dynamic processes in a natural forest, that is sudden gap formation or closure (Osunkoya and Ash, 1991, Huante and Rincon, 1998, Dalling et al., 1999, Bloor and Grubb, 2004, Dalling et al., 2004). We experimentally forced seedlings of the Dipterocarpaceae family into altered carbon balance by ma-

nipulating light environments in a shadehouse experiment. In addition, we exposed seedlings to sudden light changes by translocating them between light environments during the course of the experiment. We tested how gap dynamics with respect to changes in light affect seedling growth and if growth is inversely related to non-structural carbohydrate reserves, the sum of starch and soluble sugars (Chapin et al., 1990).

The method to measure concentrations of non-structural carbohydrates in tropical trees, seedlings and saplings (Yasman, 1995, Ichie et al., 2005, Myers and Kitajima, 2007) was commonly the phenol/sulphuric acid colorimetric assay (Ashwell, 1966). However, this approach does not allow separation of the relative contribution of the different sugar types (Hall, 2003). Simple soluble sugars (e.g. glucose, fructose and polyols) can be masked by more complex sugar compounds (e.g. starch, sucrose) when using this separation technique. Therefore the importance of single sugars may have been underestimated, even when present in large amounts. Here we used a more extensive approach to identify individual components of non-structural carbohydrates. We were interested to identify yet unknown simple sugars, quantify their relative and absolute contribution to total carbon stores in tropical dipterocarp seedlings and test if they respond to changes in the light environment.

We hypothesise that the proposed trade-off for resource allocation into either current growth or carbohydrate reserves for prolonged survival depends on: (1) an altered light environment that simulated gap formation and closures; (2) specific traits of the tree species that were further separated into generalists, shade tolerating or light demanding species; (3) plant physiological processes that were measured at the level of individual carbohydrate components.

## 7.4 Material and Methods

### 7.4.1 Experimental set-up

Our study site (N05°05'20" E117°38'32", 102 m.a.s.l.) was located in the Malua Forest Reserve in the eastern part of the province of Sabah in Malaysian northern Borneo. The shadehouse experiment was situated in logged lowland mixed dipterocarp forest, that is aseasonal with an annual rainfall of approximately 3000 mm during the measurement period (2004-2008) (Chapter 1). About 50% of the upper canopy and the emergent trees in undisturbed forest is characterised by members of the Dipterocarpaceae (dipterocarps) family (genus Anisoptera, Dipterocarpus, Dryobalanops, Hopea, Shorea, Parashorea) (Wyatt-Smith, 1995). The study species all belonged to the dipterocarps which build the majority of commercial timber extracted from this region (Symington, 1943, Ashton, 1982). Six climax species that are native to Sabah and widely used for forest rehabilitation (Sabah Forestry Departement, 2008) formed part of the experiment: *Dryobalanops lanceolata* Burck, *Hopea nervosa* King, *Shorea macroptera* Dyer, *Shorea argentifolia* Sym., *Shorea leprosula* Miq., *Shorea parvifolia* Dyer. Four of them are classified as either endangered (*Dryobalanops lanceolata, Shorea argentifolia and Shorea leprosula*) or critically endangered (*Hopea nervosa*) according to the IUCN red list (2008) and it is therefore of particular interest to study their ecology. We selected species based on seedling availability and that belong to expected shade tolerators (*Hopea nervosa, Shorea macroptera*), generalists (*Dryobalanops lanceolata*) and light demanders (*Shorea argentifolia, Shorea leprosula, Shorea parvifolia*) according to their wood density (Newman et al., 1998) and previous ecophysiological measurements (Moad, 1992, Zipperlen, 1997, Clearwater et al., 1999). All seedlings were grown from seeds of wild fruiting trees and raised under nursery conditions (11% full sunlight) at the study site.

### 7.4.2 Study design

A total of fifteen shadehouses (4 x 6 x 5 m) were alligned in five blocks of three shadehouses, randomly allocated to one of 3 light levels (see below). In order to minimise self shading blocks were sited along an east-west line with 3 m space between the houses and >10 m between blocks. Within shadehouses, seedlings were spaced 0.3 m apart. To reduce the effect of herbivory, pots were located 0.3 m above ground and wire mesh protected the seedlings from mammal damage. We simulated three light environments by using a triple, a double and a single layer of 70% black shade cloth (mean ± SEM): the forest understorey (Dark; 2.6 ± 0.6% full sunlight; 11.7 ± 2.3 µmol $s^{-1}$ $m^{-2}$), a small gap (Medium; 10.8 ± 1.3% full sunlight; 42.9 ± 4.9 µmol $s^{-1}$ $m^{-2}$) and a large gap (Light; 32.9 ± 4.5% full sunlight; 127.5 ± 13.2 µmol $s^{-1}$ $m^{-2}$).

To minimize intraspecific variation in initial size we chose seedlings of the same age (18 months) and a similar height (0.5 m). Seedlings were transplanted into black polyethylene bags (0.3 x 0.4 m) using standard, shredded topsoil. In order to prevent roots from being damaged, seedlings were kept in the original soil while transplanting. Seedlings were watered twice daily (morning and late afternoon) to avoid drought stress and fertilized twice during the course of the experiment with 2.5 g NPK slow release fertilizer (Osmocot, USA). Further they were relocated every month within each shadehouse to avoid positioning effects. Four individuals of each of six species in every shade house (n = 360) were present at start in August 2006. For the first 155 days all seedlings were kept under constant light environment (Dark, Medium or Light). For the next 165 days one individual was kept in the constant light environment as a control and two were translocated to either of the other two light environments (Dark-Medium, Dark-Light, Medium-Dark, Medium-Light, Light-Dark, Light-Medium). During the translocation at day 155 all seedlings (constant and translocated) were moved outside the shadehouses and relocated back into the shadehouses to avoid differences due to movement between the experimental treatments. We performed non-destructive measurements of diameter, height and number of leaves on all seedlings at day 0, 98, 155

(translocation) and 320 of the experiment. Randomly chosen seedlings were harvested on day 0 (initial harvest, n = 80) and 155 (second harvest, n = 90) to allometrically predict root, shoot and leaf mass and total leaf area of the non-destructively measured seedlings of the experiment. At both harvests allometries derived across species resulted in best predictions, further we used light environment specific allometries for day 155. All seedlings were harvested, separated into root, shoot and leaf mass and oven-dried at 60° degree Celsius for one week until constant mass.

### 7.4.3 Total mass growth estimation

We use two general approaches for growth analysis here: (1) a linear mixed effects model of initial size-corrected average relative growth rate, where size correction is done by including initial size as a covariate in the mixed effects model and growth is then predicted for an average seedling mass; (2) a non-linear mixed effects model analysing growth as a power function of mass (following equation 6 below). Models were fitted for (1) with the *lmer* function of the *lme4* package (Bates and Maechler, 2009, Bates, 2005) and for (2) with the *nlme* function of the *nlme* package (Pinheiro and Bates, 2000) in R 2.9.1 (R Development Core Team, 2009). Standard errors for (1) were calculated with the *sim* function of the *arm* package (Gelman et al., 2009). For (2) the standard errors from the *nlme* summary were too wide and we therefore report only the estimated mean (Table 6). This is most likely due to the large variation in our data (Hubbell, 2005) (although log transforming the data or weighting the variance according to the mean did not result in better estimations) and the fact that we only had three observed estimations of mass (day 98, 155, 320) over time (Bates, pers. comm.). Neither the (1) linear model, nor the (2) non-linear power function analysis can incorporate the initial decline in size (growth analysis methods are designed to model positive growth) (Fig.15).

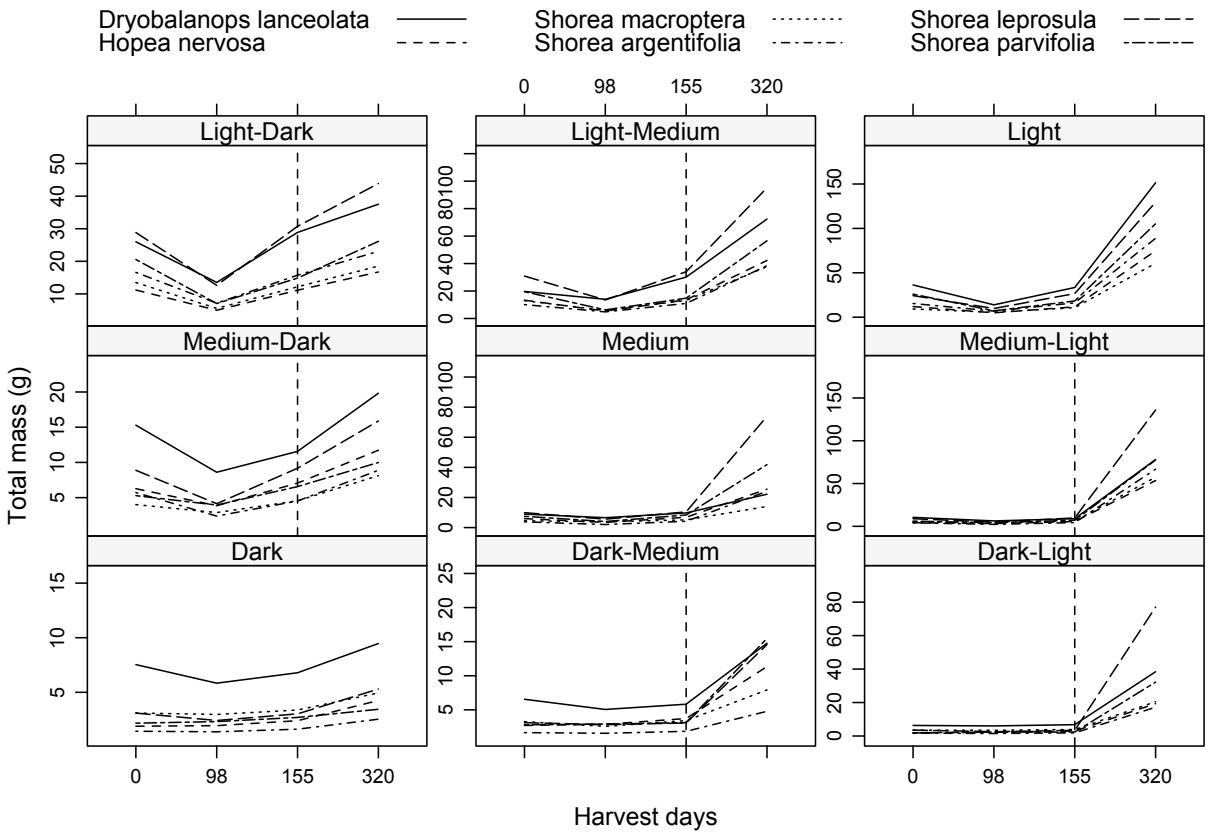


Figure 15 Overview of total mass growth in constant light conditions (Dark, Medium, Light) and with translocation (dottet vertical line) between light conditions at day 155 (Dark-Medium, Dark-Light, Medium-Dark, Medium-Light, Light-Dark, Light-Medium). Seedlings were destructively harvested at day 0, day 155, day 320 and non-destructively measured at day 98. Note the initial decline in mass from day 0 to day 155.

While we are developing more sophisticated mechanistic approaches that can incorporate negative responses following Turnbull et al. (2008), for the methods used here we must restrict the formal analysis to the period of positive growth from day 98 and omit the first measurement (day 0).

The initial size-corrected average relative growth rate with initial mass as a covariate was derived from the general model (Hunt, 1990):

$$RGR = \frac{\log_e W_2 - \log_e W_1}{T_2 - T_1} \quad (5)$$

RGR is calculated as the change in log mass, divided by the time interval ($T_2$-$T_1$). Initial size-corrected average relative growth rate does control for differences in initial mass, but is only correct if the instant

Table 6: Overview of size-corrected average relative growth rates (RGR) calculated with two general approaches: (1) Linear mixed effects model (where size correction is done by including initial size as a covariate) and (2) Non-linear mixed effects model analysing growth as a function of mass. M0: predicted starting mass (g), $\alpha$: an allometric constant, $\beta$: a scaling exponent that defines the extent to which mass is multiplying during growth. See equations in the text for the calculation of the two relative growth rates. Mean ± SEM are reported for all six species and across the three light environments. * Note that M0 was estimated as negative (-0.01) for *Hopea nervosa* in the light environment and was changed to positive (0.01) to calculate the $RGR_c$.

| Species | Light environment | RGR[1] | M0 | $\alpha$ | $\beta$ | $RGR_c$[2] |
|---|---|---|---|---|---|---|
| ***Dryobalanops lanceolata*** | **Dark** | 0.001 ± 0.0004 | 4.13 | 0.0053 | 0.6702 | 0.0033 |
| | **Middle** | 0.005 ± 0.0003 | 2.96 | 0.0149 | 0.6726 | 0.0104 |
| | **Light** | 0.008 ± 0.0004 | 1.89 | 0.0380 | 0.6748 | 0.0309 |
| ***Hopea nervosa*** | **Dark** | 0.002 ± 0.0004 | 1.58 | 0.0058 | 0.6702 | 0.0050 |
| | **Middle** | 0.005 ± 0.0003 | 0.75 | 0.0162 | 0.6726 | 0.0178 |
| | **Light** | 0.009 ± 0.0004 | 0.01* | 0.0414 | 0.6748 | 0.3461 |
| ***Shorea macroptera*** | **Dark** | 0.001 ± 0.0004 | 2.48 | 0.0042 | 0.6702 | 0.0031 |
| | **Middle** | 0.004 ± 0.0003 | 1.37 | 0.0116 | 0.6726 | 0.0105 |
| | **Light** | 0.008 ± 0.0004 | 0.35 | 0.0296 | 0.6748 | 0.0416 |
| ***Shorea argentifolia*** | **Dark** | 0.002 ± 0.0004 | 0.69 | 0.0062 | 0.6702 | 0.0070 |
| | **Middle** | 0.006 ± 0.0003 | 0.35 | 0.0174 | 0.6726 | 0.0244 |
| | **Light** | 0.009 ± 0.0004 | 0.05 | 0.0443 | 0.6748 | 0.1209 |
| ***Shorea leprosula*** | **Dark** | 0.003 ± 0.0004 | 1.38 | 0.0074 | 0.6702 | 0.0067 |
| | **Middle** | 0.006 ± 0.0003 | 0.75 | 0.0207 | 0.6726 | 0.0228 |
| | **Light** | 0.010 ± 0.0004 | 0.17 | 0.0528 | 0.6748 | 0.0941 |
| ***Shorea parvifolia*** | **Dark** | 0.002 ± 0.0004 | 1.61 | 0.0059 | 0.6702 | 0.0050 |
| | **Middle** | 0.006 ± 0.0003 | 0.87 | 0.0163 | 0.6726 | 0.0171 |
| | **Light** | 0.009 ± 0.0004 | 0.18 | 0.0417 | 0.6748 | 0.0722 |

relative growth rate does not change with mass and is therefore size independent (West et al., 1920, Hunt, 1990, South, 1995). However, as trees increase in mass the percentage in growth tends to decrease, this trend of size-related growth differences is not captured by calculating an initial size-corrected average RGR, in addition a conventional average RGR does not correct for size when this assumption is incorrect (Turnbull et al., 2008). A more adequate method is to fit a power law using non-linear regression (or mixed effects models) which can be described as a semi-mechanistic model. The advantage is that this model allows determination of the rate of mass growth (β). If β is approximately one this implies that the mass exponent is greater than 100%, which is not feasible for biological systems. We expected β to be positive and less than 1 to allow for subexponential and therefore slowing growth (Pacala et al., 1994, West et al., 1997). Model selection was based on the fit of the predicted growth curve to the observed data as well as selecting for biologically appropriate growth parameters. We estimated mass growth over time for the constant light environments (Dark, Medium, Light) as:

$$\frac{dM}{dt} = \alpha M^{\beta} \tag{6}$$

Where change in mass (dM/dt) is estimated by mass at a given time (M), an allometric constant (α) and a scaling exponent (β). The closed form solution of the power law is written as:

$$M_t = (M_0^{1-\beta} + e^{\alpha}(1-\beta)x)^{1/(1-\beta)} \tag{7}$$

Where the intercept (M0) is predicted mass at day 0, α is an allometric constant and x is time (days after experimental start). The size-corrected relative growth rate ($RGR_c$: $g\ g^{-1}\ day^{-1}$) from the power law was calculated as:

$$RGR_c = \frac{1}{M}\frac{dM}{dt} \quad \text{then;} \quad \alpha = M_0^{(\beta-1)}. \tag{8}$$

We related growth parameters derived from the initial size-corrected average RGR and a size-corrected power law relative growth rate (Power law RGR) to illustrate the differences (Fig.S1). For subsequent growth predictions we used mean estimates derived by the power law to calculate seedling mass over time. The size-corrected growth rate allowed us to test if the proposed trade-off between seedling growth and non-structural carbohydrate reserves is independent of seedling size (Myers and Kitajima, 2007).

### 7.4.4 Total mass growth prediction

To test for a trade-off between seedling growth and carbohydrate reserves we selected four out of the nine light environments, because we expected that changes are most likely to be observed in the extreme constant light environments (Dark and Light) and translocations thereof (Dark-Light, Light-Dark). We present change in mass (Δ mass), calculated as the predicted total mass (see below) minus observed mass. For example, a seedling started off growing in the dark condition for 155 days and was then translocated to the light condition for the remaining 165 days (Dark-Light), finally it was destructively harvested (observed total mass). To calculate its predicted total mass at day 155 we took growth parameters derived from the power law (M0, $\alpha, \beta$) for this particular species under dark conditions (Table 6). Then we took the predicted total mass at day 155 plus the growth parameters from the power law for this particular species under light condition to calculate its final predicted mass at day 320 (predicted total mass). As a control we predicted the seedling mass for the constant light environments (Dark, Light), expecting that the observed and the predicted mass correspond.

### 7.4.5 Extraction of total non-structural carbohydrates

Wood samples from the lower part of the main seedling stem were used for carbohydrate identification and quantification, since stem tissue was shown to have higher concentrations of non-structural carbo-

hydrates compared to roots in dipterocarp seedlings (Yasman, 1995). Samples were collected at the final harvest only (day 320), transported to the laboratory at the collecting day and oven-dried at 60° degree Celsius for one week until constant mass. Samples were ground to fine powder in a ball mill (Tissue Lyser by Qiagen, Germany). Extractions were conducted twice in 1ml of 80% and 20% ethanol and twice in 1 ml $dH_2O$ (Peters et al., 2007). For each extraction, samples were heated at 80°C for 10 min, placed on ice for 2 min, and centrifuged at 15,000 g in a bench top centrifuge for 5 min. The supernatants of all extraction steps were pooled and adjusted to 6ml with $dH_2O$. Water-soluble carbohydrates (sucrose, fructose, glucose, fractose, myo-inositol and polyols) were then identified and quantified by HPLC-PAD (Peters and Keller, 2009). The remaining pellets were dried at 55°C to remove residual EtOH and further used to quantify starch.

### 7.4.6 Quantification of starch

We used the Enzytec starch kit for food analysis to quantify starch (R-Biopharm, Germany). Pellets were resolubilized in 5ml bidestilled water and starch gelatinization was performed at 110°C for 30 min. Thereafter, 20 µl were mixed with 20 µl AGS containing α-amyloglucosidase and α-amylase and incubated at 60°C for 30 min. 120 µl $dH_2O$ was added and remaining plant parts were removed at 15,000 g in a bench top centrifuge for 10 min. 120 µl of the supernatant was transferred to a well of a microtiter plate (Greiner, Huber & Co AG, Switzerland) and mixed with 80 µl of solution #1 (containing NADP+) for the blank measurement. The enzymatic reaction was started with 1.5 µl of solution #2 (containing hexokinase and glucose-6-phosphate dehydrogenase). Absorptions were measured after 6 min for every 2 min (reaction peak at 14 min). We used a glucose (Fluka, Switzerland) standard row for calibrating the stem samples and report starch as $glucose_{eq}$ (McCready, 1950). Starch quantification was performed on a Spec-

tra Max M2 plate reader (Bucher Biotec, Switzerland) using the SoftMax Pro 4.7.1 (Molecular devices, USA).

### 7.4.7 Separation and quantitation of soluble sugars

Aliquots of 50 µl were desalted and analysed by HPLC-PAD. A Ca/Na-moderated ion partitioning carbohydrate column was used to separate carbohydrates (Benson BC-100 column, 7.8x300 mm; Benson Polymeric, Reno, NE, USA). It was operated at 90°C and isocratically eluted with 0.005% (w/v) $Ca/Na_2$ – EDTA at a flow rate of 0.6 ml $min^{-1}$. The BC-100 chromatographic system consisted of a Gynkotek model 480 High Precision Pump, a Gynkotek Gina 50 autosampler, the Chromeleon chromatography software package (version 6.4; Dionex, Olten, Switzerland), and a Jones column temperature controller (Ercatech, Berne, Switzerland). Carbohydrates were detected after post-column addition of NaOH (300 mM, 0.6 ml $min^{-1}$) using an ESA Coulochem II electrochemical detector (ESA, Cambridge, MA, USA), operated with an ESA 5040 analytical cell. Soluble carbohydrate peaks of the samples (sucrose, fructose, glucose, myo-inositol and polyol) were integrated using the Chromeleon software package (version 6.4), against a series of 5 nmol standard sugars (Sigma Aldrich, Switzerland). The quantity of standard sugars used corresponded to the linear response range of both chromatographic systems.

### 7.4.8 Delipification of extracts

Representative samples were tested to determine if lipophilic substances (such as glycosilated secondary plant products and glycolipids) were in the samples using a methanol-activated reverse-phase cartridge ($C_{18}$ Sep-Pak classic, 380 mg solid phase; Waters, Switzerland). The HPLC profiles of non-delipidated and delipidated extracts were identical (data not shown), therefore we concluded that delipification was not a necessary step to include.

### 7.4.9 Identification of Iditol

Polyols, also known as sugar alcohols occur across microbial, animal and fungal systems and in plants (Loescher and Everard, 1996). Seventeen different types are known at present, whereby at least five have been shown to occur in higher plants (Bieleski, 1982): Sorbitol, Mannitol, Galactitol, Iditol and Allitol. Iditol could only be identified with great uncertainty when using HPLC-PAD, since retention time was similar to other sugar alcohols (Xylitol, Alditol and Threitol) presented in (Adams et al., 1992). To confirm the identity of the yet unknown polyol in the samples we analyzed them by Gas chromatography/ Mass spectrometry (GC/MS). Hereby, the individual sugar components were separated according to their retention time (GC) and their fragmented mass structure (MS). Polyols are strongly non volatile due to high amounts of alcohol groups. Therefore the volatility had to be increased by adding apolar groups. 1-Trimethylsilyl-imidazole (TMS) (Fluka, Switzerland) was used to derivatize the samples at 60°C for 30 min (adding $–Si(CH_3)_3$). As solvent we used pyridine. The samples run on a DB-5 column (J&W, USA) attached to a Trace GC ultra gas chromatograph (Finnigan, USA) with helium as carrying gas and an integrated Trace DSQ mass spectrometer (Finnigan, USA). 1 µl of the derivatized sample was injected and vaporization was performed at a gradient of 8°C $min^{-1}$ from 60 to 300°C. The unknown polyol (retention time: 19.88 min) in the experimental samples was compared to a series of standard polyols (Arabitol, Erythritol, Threitol, Xylitol, Mannitol, Sorbitol, Dulcitol and Iditol). Particularly the last four sugar alcohols had a similar retention time (19.75-19.90 min) due to their stereoisometry (Molar mass: 182.17). We used the WADA (world anti-doping agency) range of tolerance to identify the unknown polyol according to its mass structure. Hereby, a relative intensity ≥50% of the base peak has an absolute tolerance of ±10%, and for the range between <50% and ≥25% the relative tolerance is ±15% (Rivier, 2003). Two fractions (217 and 319.1) with the highest mass to charge ratio (m/z) could only be assigned to the Iditol standard for eight random samples, confirming that the unknown polyol is indeed Iditol (Table S4).

## 7.5 Results

### 7.5.1 Total mass growth estimation

Our data shows an initial decline in mass growth from day 0 to day 98 across all species (Fig.15). The negative growth is predominant in the dark condition, where mass growth was small across the length of the experiment. The relationship between initial size-corrected average relative mass growth and size-corrected relative mass growth (Power law $RGR_c$) showed that the power law estimated higher growth rates across all light environments and species (Table 6). The interaction between light environments and species was not significant for growth estimations derived by a model with initial size-corrected average RGR as the response (log likelihood ratio statistic: $\chi^2 = 1.7$, $p = 0.89$). However, we could not test for the interaction in a model with $RGR_c$ (estimated from the power law) as the response, since the model did not converge once the interaction was fitted. Both growth models are reported based on estimations from the main effects (species and light environment) only. The difference in growth (initial size-corrected average RGR versus Power law $RGR_c$) was predominant for *Hopea nervosa* and for the light demanding species (*Shorea argentifolia, Shorea leprosula* and *Shorea parvifolia*). *Dryobalanops lanceolata* and *Shorea macroptera* were estimated with more constant size-corrected relative growth rates across the light conditions (Fig. S1). The power law estimated the mass scaling exponent ($\beta$) at 0.67 across all constant light environments (Dark, Medium, Light) (Table 1). This is close to the two-thirds exponent of the Kleiber's law, rather than the three-quarter law proposed by West et al., (1997) and fits well with expected rates of biomass growth in plant communities. We found that the power law $RGR_c$ derived growth rates were more flexible to species and light specific changes and therefore consider these estimates to test for a trade-off between seedling growth and storage of carbohydrate reserves.

### 7.5.2 Resource allocation to growth or non-structural carbohydrates

As expected, seedlings exposed to the dark had lower relative mass growth and depleted stores of non-structural carbohydrates (sum of starch and soluble sugars). When exposed to high light relative growth and non-structural carbohydrate reserves increased (Fig.16). There was significant variation in the relationship between seedling mass growth and non-structural carbohydrate reserves across the six species (log likelihood ratio statistic: $\chi^2 = 49.4$, $p < 0.0001$). In five out of six species the relationship was significantly positive from the dark to the light environment (Mean slope ± SEM): *Dryobalanops lanceolata* (330 ± 144 mg $g^{-1}$, $t = 2.3$, $p < 0.05$), *Hopea nervosa* (3541 ± 712 mg $g^{-1}$, $t = 5.0$, $p < 0.0001$), *Shorea leprosula* (792 ± 316 mg $g^{-1}$, $t = 2.5$, $p < 0.05$), *Shorea macroptera* (2736 ± 776 mg $g^{-1}$, $t = 3.5$, $p < 0.001$) and *Shorea parvifolia* (1733 ± 445 mg $g^{-1}$, $t = 3.9$, $p < 0.001$). The relation was not significant for *Shorea argentifolia* (170 ± 236 mg $g^{-1}$, $t = 0.7$, $p = 0.48$).

To test for a trade-off between carbohydrate allocation to either growth or reserves we related the change in mass (observed mass - predicted mass) (Fig.17) to measured concentrations of non-structural carbohydrates, devided into either starch or the sum of all soluble sugars. A higher difference in negative mass change after translocation indicated that a seedling allocated less resources into mass growth. We used the *gls* function in the *nlme* package (Pinheiro and Bates, 2000) for generalized least squares analysis, specifying the variance to increase as a power of the primary covariate (i.e. mass change) for each species and light translocation separately (weighted versus unweighted model; log likelihood ratio statistic: $\chi^2 = 31.0$, $p < 0.001$) (Zuur et al., 2009).

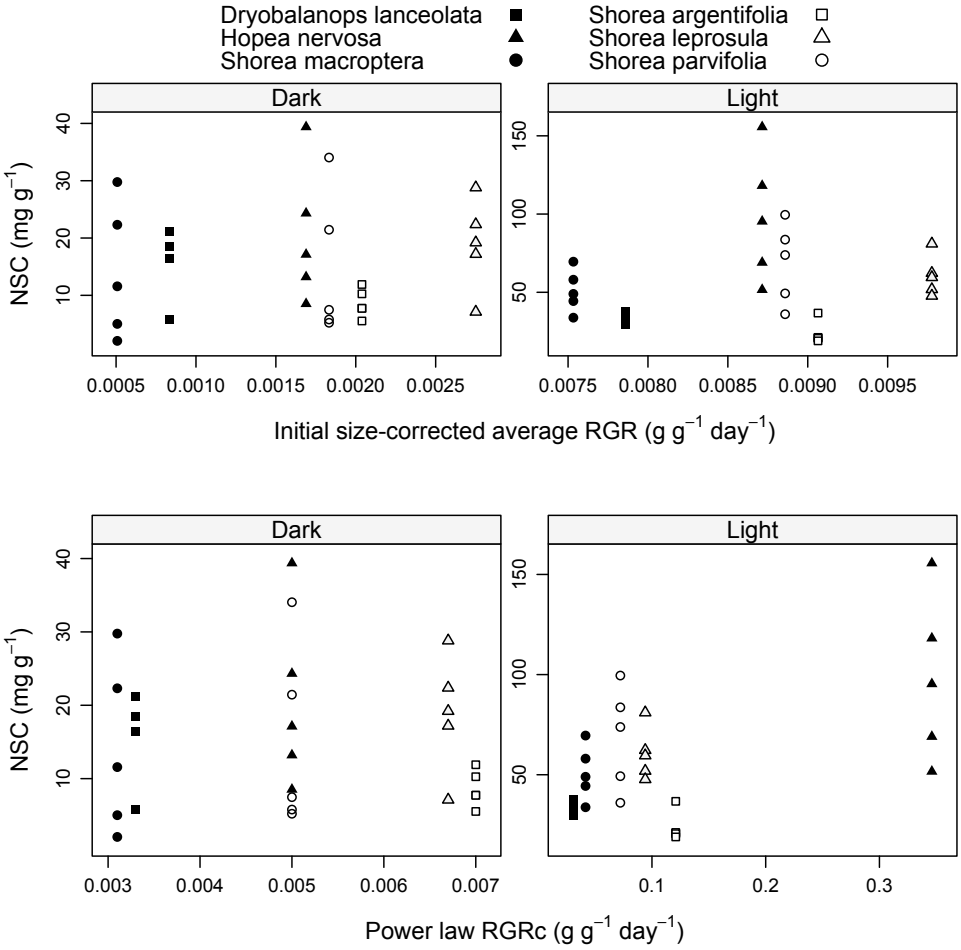


Figure 16 Relationship between non-structural carbohydrates (NSC: sum of starch and soluble sugars) and initial size-corrected average growth rate derived from a linear model, or size-corrected average growth rate derived from a power law (Power law RGR$_c$) for all six species under selected constant light conditions (Dark, Light). The expected generalist (*Dryobalanops lanceolata*) and shade tolerators (*Hopea nervosa, Shorea macroptera*) are indicated with filled characters, expected light demanders (*Shorea argentifolia, Shorea leprosula, Shorea parvifolia*) are shown with open characters. All seedlings showed lower NSC content in the dark compared to the light environment.

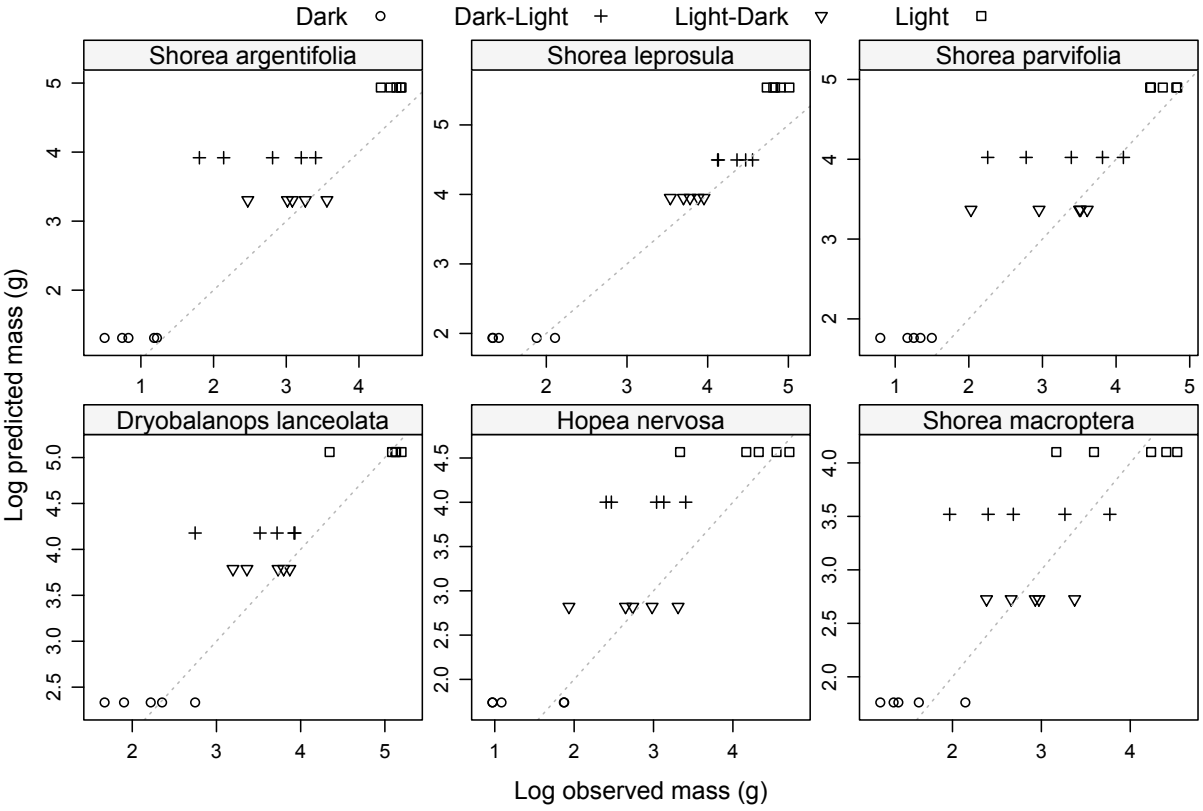


Figure 17 Relationship between predicted mass derived from the power law (Log predicted mass) and observed mass (Log observed mass) in constant light environments (Dark, Light) and with translocation between light environments (Dark-Light, Light-Dark). Dottet line (Intercept = 0, slope = 1) indicates if predicted seedling mass corresponds with observed mass. Note that mass was overpredicted for *Shorea argentifolia* and *Shorea leprosula* in the light condition (Light).

### 7.5.3 Starch

We found a significant difference for the relationship between starch concentration and change in mass growth between the six species ($F_{5,41}$ = 105.3, p < 0.0001) and between both translocations ($F_{1,41}$ = 54.2, p < 0.0001) (Fig.18). The three way interaction was not found to be significant (log likelihood ratio statistic: $\chi^2$ = 7.8, p = 0.17) and was removed from the model. The translocation from Dark-Light caused a trade-off (Mean negative slope ± SEM) between allocation to either growth or starch reserves for *Dryobalanops lanceolata* (-0.4 ± 0.2 mg $g^{-1}$, t = 2.6, p < 0.05), *Shorea macroptera* (-0.4 ± 0.11 mg $g^{-1}$, t = 3.7, p < 0.001), *Shorea argentifolia* (-0.3 ± 0.11 mg $g^{-1}$, t = 2.6, p < 0.05) and *Shorea parvifolia* (-0.2 ± 0.13 mg $g^{-1}$, t = 2.0, p < 0.1). In contrast the relationship was not found to be significant for *Hopea nervosa* (-0.1 ± 0.1 mg

$g^{-1}$, t = 0.5, p = 0.64) and *Shorea leprosula* (0.05 ± 0.12 mg $g^{-1}$, t = 0.4, p = 0.69). The translocation from Light-Dark caused a significant positive relationship (Mean slope ± SEM) between allocation to growth and starch for *Hopea nervosa* (0.2 ± 0.03 mg $g^{-1}$, t = 8.3, p < 0.0001) and *Shorea leprosula* (0.3 ± 0.04 mg $g^{-1}$, t = 9.32, p < 0.0001). The relationship was not found to be significant for the other species (Fig.18).

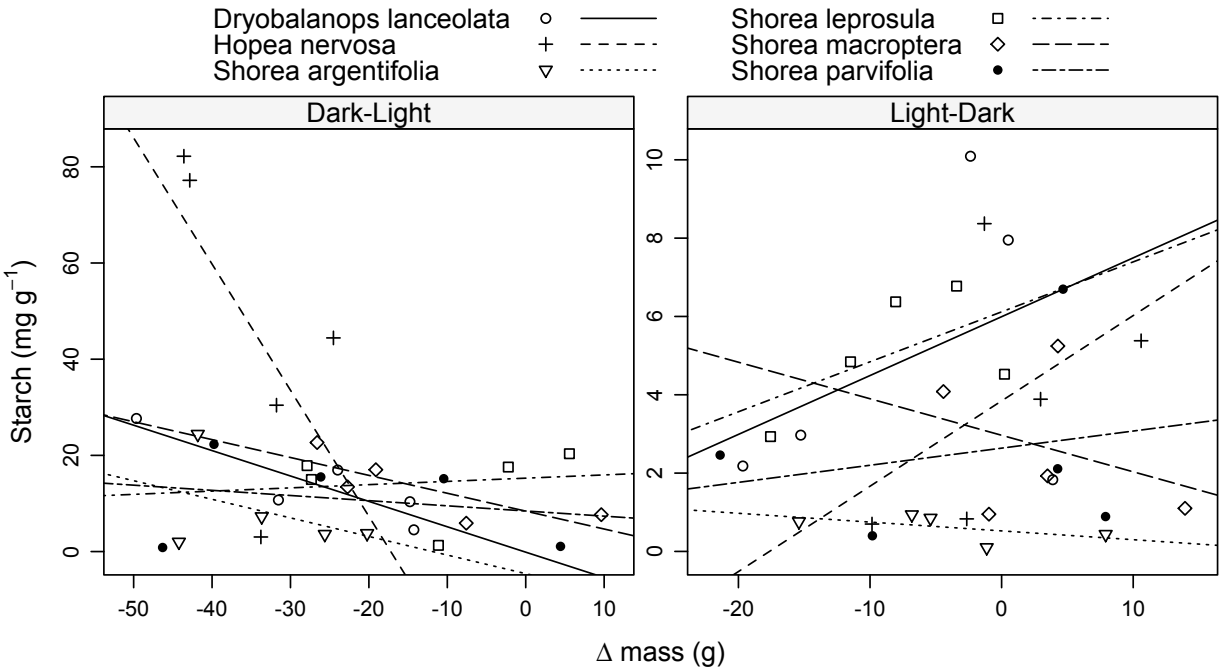


Figure 18 Correlation between starch and seedlings mass change for all six species translocated between light environments: Dark-Light and Light-Dark. Decreasing mass change indicates that seedlings adapted less well to translocation than predicted.

## 7.5.4 Soluble sugars

The relationship between soluble sugars and change in mass growth significantly differed across species ($F_{5,41}$ = 71.5, p < 0.0001) and across translocations ($F_{1,41}$ = 142.5, p < 0.0001) (Fig.19). Again, the three way interaction was not found to be significant (log likelihood ratio statistic: $\chi^2$ = 3.0, p = 0.70) and was removed from the model. The translocation from Dark-Light caused a significant trade-off (Mean negative slo-

pe ± SEM) between allocation to either growth or soluble sugars for *Dryobalanops lanceolata* (-0.7 ± 0.16 mg $g^{-1}$, t = 4.6, p < 0.0001), *Hopea nervosa* (-0.8 ± 0.39 mg $g^{-1}$, t = 2.1, p < 0.05), *Shorea macroptera* (-0.7 ± 0.36 mg $g^{-1}$, t = 1.9, p < 0.1), *Shorea argentifolia* (-0.5 ± 0.15 mg $g^{-1}$, t = 3.2, p < 0.01) and *Shorea parvifolia* (-0.4 ± 0.15 mg $g^{-1}$, t = 2.6, p < 0.05). The relationship was not found to be significant for *Shorea leprosula* (-0.15 ± 0.18 mg $g^{-1}$, t = 0.8, p = 0.43). The translocation from Light-Dark caused a significant negative relationship (Mean slope ± SEM) between allocation to either growth or soluble sugars for *Dryobalanops lanceolata* (-0.2 ± 0.08 mg $g^{-1}$, t = 2.8, p < 0.01). The relationship was found to be significantly positive for *Shorea parvifolia* (0.1 ± 0.05 mg $g^{-1}$, t = 2.2, p < 0.05) and *Shorea leprosula* (0.3 ± 0.16 mg $g^{-1}$, t = 2.1, p < 0.05). In contrast the relationship was not found to be significant for the other species.

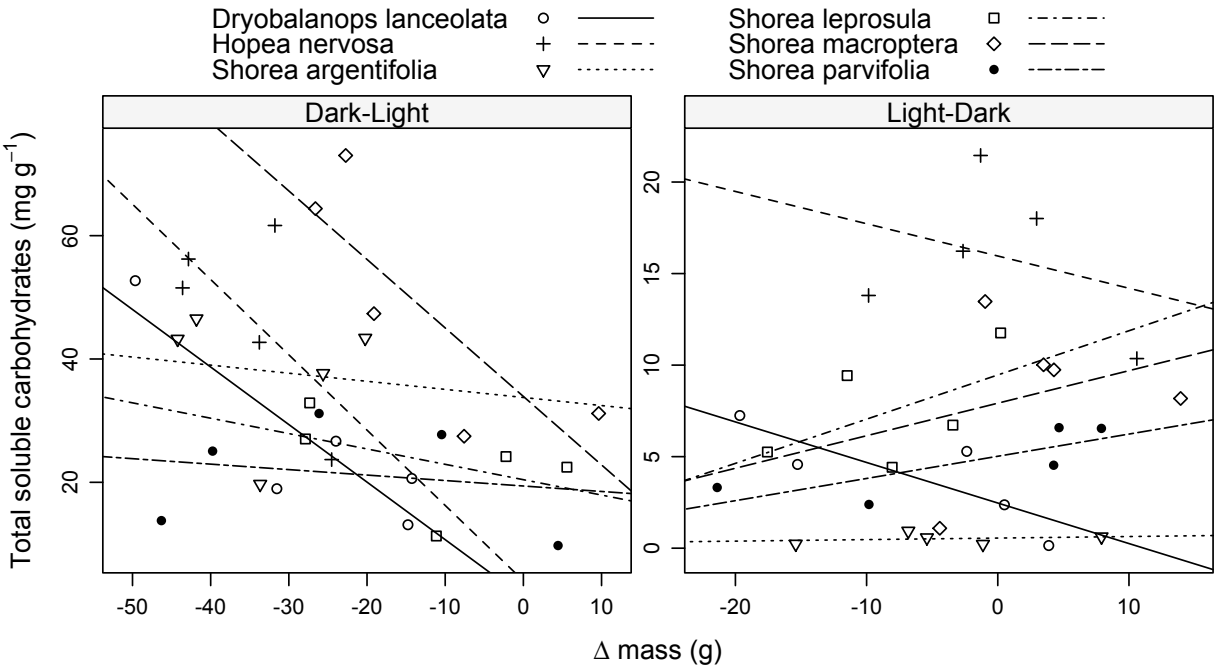


Figure 19 Correlation between total soluble carbohydrates and seedlings mass change for all six species translocated between light environments: Dark-Light and Light-Dark. Decreasing mass change indicates that seedlings adapted less well to translocation than predicted.

### 7.5.5 Polyols

Iditol—a yet unidentified sugar alcohol in tropical trees—was a major component of soluble sugars in seedlings of all six dipterocarp species. Its mean relative concentration compared to total non-structural carbohydrates ranged between 3 – 47% (mean absolute concentration: 0.1 – 17.8 mg $g^{-1}$), depending on species and light environment (Table 7). Iditol significantly differed between species ($F_{5,87}$ = 23.2, p < 0.0001) and between light environments ($F_{3,87}$ = 74.1, p < 0.0001). For *Dryobalanops lanceolata* Iditol concentration was significantly higher after increasing the light environment compared to a decrease (Dark-Light vs. Light-Dark; Mean difference ± SED: -5.6 ± 2.2 mg $g^{-1}$, t = 2.5, p < 0.05), whereby other changes in the light environment did not significantly affect Iditol concentrations. *Hopea nervosa* showed a significant increase from dark to light conditions (Dark vs. Light: 6.0 ± 2.3 mg $g^{-1}$, t = 2.6, p < 0.05) and in increased light conditions (Light-Dark vs. Dark-Light; 10.3 ± 2.0 mg $g^{-1}$, t = 5.1, p < 0.0001). For *Shorea macroptera* differences were significant between dark and light (Dark vs. Light: 6.1 ± 2.4 mg $g^{-1}$, t = 2.5, p < 0.05) and in altered light environments (Light-Dark vs. Dark-Light; 10.6 ± 2.0 mg $g^{-1}$, t = 5.4, p < 0.0001). The differences were marginally significant for constant light environments in *Shorea argentifolia* (Dark vs. Light: 4.2 ± 2.3 mg $g^{-1}$, t = 1.9, p < 0.1) but highly significant between translocated seedlings (Light-Dark vs. Dark-Light; 12.7 ± 1.9 mg $g^{-1}$, t = 6.6, p < 0.0001). In *Shorea leprosula* a significant difference could only be observed for the translocations (Light-Dark vs. Dark-Light; 7.6 ± 2.5 mg $g^{-1}$, t = 3.0, p < 0.01). For *Shorea parvifolia* we found a significant difference for both, the constant (Dark vs. Light: 13.5 ± 2.4 mg $g^{-1}$, t = 5.7, p < 0.0001) and the translocated seedlings (Light-Dark vs. Dark-Light; 11.8 ± 2.1 mg $g^{-1}$, t = 5.6, p < 0.0001). Across all species Iditol concentrations were higher in light condition compared to the dark (Dark vs. Light: 6.7 ± 1.2 mg $g^{-1}$, t = 5.5, p < 0.0001). In addition Iditol concentrations were higher after increasing the light environment, compared to decreasing the light environment (Mean difference ± SED: 10.5 ± 0.9 mg $g^{-1}$, t = 12.0, p < 0.0001). Whereby the previous light

environment did not affect final Iditol concentration in the dark (Light-Dark vs. Dark; Mean difference ± SED: 0.9 ± 0.7 mg $g^{-1}$, t = 1.2, p = 0.23), the difference was significant for the light condition (Dark-Light vs. Light; Mean difference ± SED: -2.9 ± 1.3 mg $g^{-1}$, t = 2.2, $p < 0.05$).

## 7.6 Discussion

We provide first evidence for a trade-off between size-corrected change in mass growth and allocation of starch and soluble sugars in tropical dipterocarp seedlings. For four species (*Dryobalanops lanceolata, Shorea macroptera, Shorea argentifolia* and *Shorea parvifolia*) we found that greater proportional allocation to carbohydrate reserves may be a direct physiological cause of lower growth after a gap opening (Dark-Light). For one species (*Shorea leprosula*) we could not detect a negative relationship between mass growth and carbohydrate reserves after a gap opening (Dark-Light), but for the same species we found a positive relationship between mass growth and carbohydrate reserves after a gap closure (Light-Dark). For one species (*Hopea nervosa*) we found a trade-off for mass growth and soluble sugars after a gap opening (Dark-Light), but a positive relationship between mass growth and starch after a gap closure (Light-Dark). In addition we found a significant positive relationship between mass growth and soluble sugars after gap closure (Light-Dark) in *Shorea parvifolia*.

Our findings suggest that dipterocarps pursue unequal carbohydrate allocation strategies during canopy gap dynamics. Seedlings of four species allocated a larger share of their photosynthates into either mass growth or carbohydrate reserves (starch and soluble sugars) after a gap opening. Carbohydrate allocation to reserves may allow a seedling to prolong survival under stress conditions, for example if a seedling is overshadowed by a faster growing competitor (a gap closure event), after insect or pathogen attack (Renaud and Mauffette, 1991, Liu and Tyree, 1997), or as a result of limiting abiotic conditions (Tattini et al., 1996).

Table 7: Overview of non-structural carbohydrates for seedlings of all six species in two constant (Dark, Light) and two translocated (Dark-Light, Light-Dark) light environments. Starch, total soluble sugars (TSS), Iditol and non-structural carbohydrates (NSC). Mean ± SEM (mg $g^{-1}$) are reported for all measures. Percentage of total non-structural carbohydrates is shown in parentheses.

| | | *Dryobalanops lanceolata* | | *Hopea nervosa* | | *Shorea macroptera* | | *Shorea argentifolia* | | *Shorea leprosula* | | *Shorea parvifolia* | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Dark** | | | | | | | | | | | | | |
| | **Starch** | 5.0 ± 1.5 | (29.9) | 3.2 ± 1.6 | (15.5) | 4.4 ± 2.3 | (31.2) | 1.6 ± 0.4 | (18.6) | 2.8 ± 1.1 | (14.8) | 2.0 ± 1.2 | (13.5) |
| | **TSS** | 11.7 ± 2.6 | (70.1) | 17.4 ± 3.9 | (84.5) | 9.7 ± 3.1 | (68.8) | 7.0 ± 1.2 | (81.4) | 16.2 ± 3.6 | (85.2) | 12.8 ± 5.4 | (86.5) |
| | **Iditol** | 1.1 ± 0.2 | (6.6) | 2.1 ± 0.5 | (10.2) | 0.8 ± 0.2 | (5.7) | 2.2 ± 1.3 | (25.6) | 8.8 ± 3.0 | (46.6) | 4.7 ± 2.8 | (31.8) |
| | **NSC** | 16.7 ± 2.8 | (100) | 20.6 ± 5.4 | (100) | 14.1 ± 5.3 | (100) | 8.6 ± 1.1 | (100) | 19.0 ± 3.6 | (100) | 14.8 ± 5.7 | (100) |
| **Dark-Light** | | | | | | | | | | | | | |
| | **Starch** | 14.0 ± 3.9 | (34.6) | 47.5 ± 14.8 | (50.2) | 13.3 ± 3.1 | (21.4) | 7.0 ± 4.4 | (16.1) | 18.6 ± 1.3 | (41.4) | 8.0 ± 3.2 | (28.2) |
| | **TSS** | 26.4 ± 6.9 | (65.4) | 47.2 ± 6.6 | (49.8) | 48.7 ± 8.9 | (78.6) | 36.4 ± 6.4 | (83.9) | 26.3 ± 1.8 | (58.6) | 20.4 ± 4.0 | (71.8) |
| | **Iditol** | 5.4 ± 1.7 | (13.4) | 12.0 ± 2.6 | (12.7) | 10.8 ± 2.5 | (17.4) | 12.5 ± 2.4 | (28.8) | 13.7 ± 1.4 | (30.5) | 12.9 ± 1.7 | (45.4) |
| | **NSC** | 40.4 ± 10.6 | (100) | 94.7 ± 17.5 | (100) | 62.0 ± 11.4 | (100) | 43.4 ± 9.3 | (100) | 44.9 ± 1.2 | (100) | 28.4 ± 7.2 | (100) |
| **Light-Dark** | | | | | | | | | | | | | |
| | **Starch** | 5.0 ± 1.7 | (56.2) | 3.8 ± 1.4 | (19.2) | 2.7 ± 0.9 | (24.1) | 0.6 ± 0.2 | (54.5) | 5.1 ± 0.7 | (40.5) | 2.5 ± 1.1 | (34.7) |
| | **TSS** | 3.9 ± 1.2 | (43.8) | 16.0 ± 1.9 | (80.8) | 8.5 ± 2.0 | (75.9) | 0.5 ± 0.1 | (45.5) | 7.5 ± 1.4 | (59.5) | 4.7 ± 0.8 | (65.3) |
| | **Iditol** | 0.3 ± 0.1 | (3.4) | 1.9 ± 0.3 | (9.6) | 1.0 ± 0.3 | (9) | 0.1 ± 0.01 | (9.1) | 4.6 ± 0.8 | (36.5) | 1.6 ± 0.5 | (22.2) |
| | **NSC** | 8.9 ± 2.2 | (100) | 19.8 ± 2.8 | (100) | 11.2 ± 1.8 | (100) | 1.1 ± 0.3 | (100) | 12.6 ± 1.4 | (100) | 7.2 ± 1.7 | (100) |
| **Light** | | | | | | | | | | | | | |
| | **Starch** | 16.5 ± 3.6 | (48.8) | 50.0 ± 15.2 | (51.1) | 15.1 ± 2.5 | (29.7) | 8.4 ± 3.7 | (35.4) | 35.0 ± 9.3 | (57.8) | 31.7 ± 7.6 | (46.3) |
| | **TSS** | 17.3 ± 2.1 | (51.2) | 47.9 ± 9.2 | (48.9) | 35.8 ± 6.3 | (70.3) | 15.3 ± 1.0 | (64.6) | 25.5 ± 5.4 | (42.2) | 36.8 ± 6.2 | (53.7) |
| | **Iditol** | 3.7 ± 0.1 | (10.9) | 7.7 ± 1.9 | (7.9) | 6.9 ± 0.9 | (13.6) | 6.2 ± 0.3 | (26.2) | 12.1 ± 2.4 | (20) | 17.8 ± 2.9 | (26) |
| | **NSC** | 33.8 ± 1.7 | (100) | 97.9 ± 18.3 | (100) | 50.9 ± 6.1 | (100) | 23.7 ± 3.3 | (100) | 60.5 ± 5.8 | (100) | 68.5 ± 11.5 | (100) |

An evident strategy for seedlings exposed to a gap closure would be to either invest resources into growth to overcome the limiting factor (for example a competitor or a dead branch that overshadows the seedling), or to reduce growth to persevere until the environmental conditions are favourable. We could not observe such a general trend for dipterocarp seedlings exposed to a gap closure. All species showed low growth rates and depleted carbohydrate stores in the dark. Instead, we found that seedlings of three species allocated energy into mass growth and carbohydrate after a gap closure (Light-Dark), whereby the relationship was particularly strong for *Hopea nervosa* and *Shorea leprosula* allocating energy into mass growth and starch. It is possible that seedlings of these species used carbohydrate stores from the roots to overcome growth limiting light decreases. As we did not measure root carbohydrate stores we could not test for this directly. Another explanation could be that the seedlings were not yet exposed to the below-light compensation point in the dark condition (3% full sunlight; 12 μmol $s^{-1}$ $m^{-2}$) (Eschenbach et al., 1998). None of the seedlings died during the experiment and all six species showed relatively high non-structural carbohydrate reserves in the dark condition (Table 7). In addition all seedlings showed lower reserves after a light decrease (Light-Dark) compared to the dark condition (Dark), indicating that adaptation to the dark further reduced carbohydrate stores across all species. However, testing for a growth-survival life history trade-off requires a negative carbon balance (Myers and Kitajima, 2007), therefore we could not test for such an effect. Despite the differences in light requirements amongst the species we could not observe a clear trend with regard to carbohydrate allocation to either growth or reserves for different functional groups as proposed earlier (Poorter and Kitajima, 2007).

### 7.6.1 Polyols

Polyols, also known as sugar alcohols, occur across microbial, animal and fungal systems and in plants (Loescher and Everard, 1996). Seventeen different types are known at present, whereby at least five have

been shown to occur in higher plants (Bieleski, 1982): Sorbitol, Mannitol, Galactitol, Iditol and Allitol. An extensive study by Zimmermann and Ziegler (1975) revealed that polyols, in particular Sorbitol, Mannitol and Galactitol were transported in 75 out of 500 higher plant species. In polyol producing higher plants they build the major source of soluble sugars besides sucrose (Loescher and Everard, 2000). About 30% of the global primary production was estimated to go through polyols (Bieleski, 1982), however little is known about their importance in tropical regions. We present first evidence that Iditol, a yet unknown polyol in tropical trees, may contribute up to 50% to non-structural carbohydrate reserves in dipterocarp seedlings. Bieleski & Briggs (2005) found high levels (60 mg $g^{-1}$ fresh weight) of polyols in leaf tissues of Protea species across South Africa, Australia, New Zealand and South America. They reported polyols to be the dominant, single soluble compound, second only to cellulose (100 mg $g^{-1}$ fresh weight) as the end product of photosynthates in Proteaceae. Specific regulation of polyol stores and transports are suggested to depend on species, tissue, plant developmental stage and environmental conditions (Loescher and Everard, 2000). Würth et al. (2005) reported that the relative share of mobile carbon compounds was less than 10% for carbohydrates other than starch, sucrose, fructose and glucose for 17 species of tropical trees. Hence it may be that polyols are particularly important at the seedling stage. Polyols were shown to be metabolically more sequestered which may be important for stress tolerance (Loescher and Everard, 2000). For example it was shown that polyols are associated with tolerance to cold, drought, salt or temperature (Vernon et al., 1993, Holmstrom et al., 1996). We observed significantly higher Iditol concentrations in light conditions and five months after a light increase. In addition we found higher relative contribution of Iditol to non-structural carbohydrate reserves for the light demanders (*Shorea argentifolia, Shorea leprosula, Shorea parvifolia*) but not for the generalist (*Dryobalanops lanceolata*) or the shade tolerant species (*Hopea nervosa, Shorea macroptera*) (Table 7), suggesting that Iditol may also act as a light stress indicator.

To our knowledge Iditol has been reported only once in higher plants (Plouvier, 1963) in *Sorbus aucuparia* (Rowan tree). Interestingly *Sorbus aucuparia* is associated with ectomycorrhiza as is the case for South-East Asian dipterocarps. Nothing is known about factors that affect Iditol content, but Allitol, another polyol, was suggested to be an early product of photosynthesis, increasing in amount with photosynthetic activity and depleting in darkness (Hough and Stacey, 1966). Free glucose, fructose and sucrose can be rapidly and extensively metabolized to polyols. However, the conversion from polyol to sugar does not occur readily, because they are susceptible to enzymatic degradation only (Bielesky and Redgwell, 1980). This suggests that the polyol pathway of synthesis and utilization may be different and under separate control. We can only speculate about possible pathways for dipterocarps. The chemical reduction of a ketose can form a new assymetric center, thus two configurations and two polyols are possible. Depending on the enzyme involved after chemical reduction of a L-Sorbose, this can yield to both Iditol and Sorbitol. Recent studies identified a homologous sequence to the Sorbitol dehydrogenase in five species of the genus Shorea (Ishiyama, 2008). Although they did not test for the function of the sequence, this may suggest for Sorbitol in dipterocarps, which Iditol could be a metabolite of.

Polyols are also known to be involved in the carbohydrate transport between autotrophs and heterotrophs (Allen, 1992). Since environmental induced stresses in ectomycorrhiza were shown to be related to polyols (Tibbett et al., 2002), we hypothesise that Iditol may be related to stress tolerance in dipterocarp seedlings and associated ectomycorrhiza. Future studies should focus on plant physiological pathways in dipterocarps and associated ectomycorrhiza with respect to Iditol. As polyols were shown to alter stress tolerance this may yield new insights into mechanisms of tree species coexistence in tropical forests.

## 7.7 Conclusion

We conclude that seedlings of tropical dipterocarps pursue different carbohydrate allocation strategies under altered light environments. In particular we observed that seedlings of five out of six species showed a trade-off between carbohydrate allocation to either growth or reserves after a simulated gap opening. A novel approach for size-corrected plant growth analysis was presented and suggests that the found trade-off is indeed independent of seedling size. We emphasize the importance of polyols (Iditol) for plant physiological processes in dipterocarp seedlings.

## 7.8 Acknowledgements

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## 7.9 Appendix

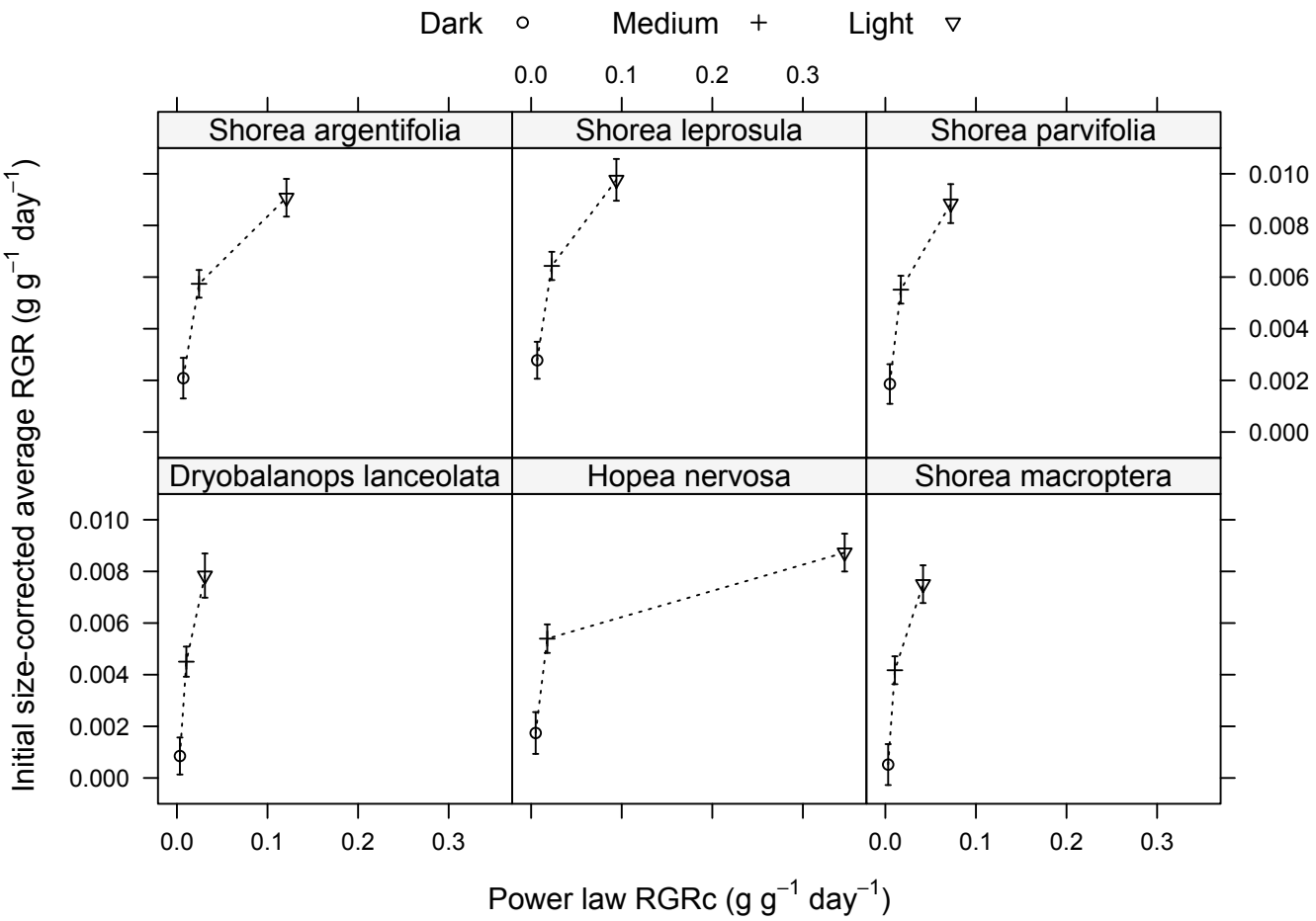


Figure S1 Relationship between initial size-corrected average relative growth rate (RGR; mean ± 95% CI) and size-corrected growth rate derived from a power law (Power law RGR$_c$). Estimated growth rates are shown for all six species and across the constant light treatments (Dark, Medium, Light).

Table S4: Overview of the GC/MS (Gas chromatography / Mass spectrometry) output for selected standards: Iditol (ID), Dulcitol (DU), Sorbitol (SO) and for eight randomly chosen samples across all species and light environments. Mass to charge ratio (m/z), relative intensity of the base peak (intensity). If intensity is ≥50% (**bold**) the absolute tolerance (**abs**) is ± 10%. If intensity is <50% and ≥25% the relative tolerance (rel) is ±15% (see text for further details).

| **Iditol standard (ID)** | | **Range** | | **Dulcitol standard (DU)** | | **Range** | | **Sorbitol standard (SO)** | | **Range** | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| m/z | intensity | **abs-** rel- | **abs+** rel+ | m/z | intensity | **abs-** rel- | **abs+** rel+ | m/z | intensity | **abs-** rel- | **abs+** rel+ |
| **217** | **72.82** | **62.82** | **82.82** | **217** | **93.09** | **83.09** | **103.09** | **217** | **50.89** | **40.89** | **60.89** |
| **319.1** | **71.31** | **61.31** | **81.31** | **319.1** | **45.88** | **36.704** | **55.056** | **319.1** | **82.95** | **72.95** | **92.95** |
| **205** | **60.61** | **50.61** | **70.61** | **205** | **46.8** | **37.44** | **56.16** | **205** | **62.78** | **52.78** | **72.78** |
| **147** | **52.91** | **42.91** | **62.91** | **147** | **53.31** | **43.31** | **63.31** | **147** | **53.43** | **43.43** | **63.43** |
| 102.9 | 35.53 | 28.424 | 42.636 | 102.9 | 43.29 | 34.632 | 51.948 | 102.9 | 34.99 | 27.992 | 41.988 |
| 307.1 | 23.24 | 18.24 | 28.24 | 307.1 | 35.65 | 28.52 | 42.78 | 307.1 | 20.29 | 15.29 | 25.29 |
| 320.2 | 19.76 | 14.76 | 24.76 | 320.2 | 12.99 | 7.99 | 17.99 | 320.2 | 22.79 | 17.79 | 27.79 |
| 218.1 | 14.57 | 9.57 | 19.57 | 218.1 | 16.91 | 11.91 | 21.91 | 218.1 | 9.46 | 4.46 | 14.46 |
| 116.9 | 12.61 | 7.61 | 17.61 | 116.9 | 12.44 | 7.44 | 17.44 | 116.9 | 12.27 | 7.27 | 17.27 |
| 206.1 | 11.55 | 6.55 | 16.55 | 206.1 | 8.58 | 3.58 | 13.58 | 206.1 | 12.53 | 7.53 | 17.53 |
| 204 | 10.44 | 5.44 | 15.44 | 204 | 12.68 | 7.68 | 17.68 | 204 | 10.98 | 5.98 | 15.98 |
| 321.1 | 8.86 | 3.86 | 13.86 | 321.2 | 5.39 | 0.39 | 10.39 | 321.2 | 10.24 | 5.24 | 15.24 |
| 74 | 8.52 | 3.52 | 13.52 | 74 | 9.04 | 4.04 | 14.04 | 74 | 7.93 | 2.93 | 12.93 |
| 148 | 8.4 | 3.4 | 13.4 | 148 | 8.42 | 3.42 | 13.42 | 148 | 8.39 | 3.39 | 13.39 |
| 191 | 8.4 | 3.4 | 13.4 | 191 | 10.37 | 5.37 | 15.37 | 191 | 8.29 | 3.29 | 13.29 |
| 189 | 8.3 | 3.3 | 13.3 | 189 | 8.13 | 3.13 | 13.13 | 189 | 9.26 | 4.26 | 14.26 |
| 132.9 | 7.66 | 2.66 | 12.66 | 132.9 | 7.89 | 2.89 | 12.89 | 133 | 6.93 | 1.93 | 11.93 |
| 128.9 | 7.18 | 2.18 | 12.18 | 128.9 | 6.94 | 1.94 | 11.94 | 129 | 7.27 | 2.27 | 12.27 |

Table S4/2: Overview of the GC/MS (Gas chromatography / Mass spectrometry) output for selected standards: Iditol (ID), Dulcitol (DU), Sorbitol (SO) and for eight randomly chosen samples across all species and light environments. Mass to charge ratio (m/z), relative intensity of the base peak (intensity). If intensity is ≥50% (**bold**) the absolute tolerance (**abs**) is ± 10%. If intensity is <50% and ≥25% the relative tolerance (rel) is ±15% (see text for further details).

| ***Hopea nervosa*** | | **Dark-Light** | ***Dryobalanops lanceolata*** | | **Dark-Dark** | ***Shorea parvifolia*** | | **Light-Light** | ***Shorea parvifolia*** | | **Light-Light** |
|---|---|---|---|---|---|---|---|---|---|---|---|
| m/z | intensity | range | m/z | intensity | range | m/z | intensity | range | m/z | intensity | range |
| **217** | **72.78** | **ID** | **217** | **70.55** | **ID** | **217** | **72.28** | **ID** | **217** | **71.87** | **ID** |
| **319.1** | **70.67** | **ID** | **319.1** | **65.09** | **ID** | **319.1** | **72.06** | **ID** | **319.1** | **72.73** | **ID** |
| **205** | **59.86** | **ID/SO** | **205** | **59.01** | **ID/SO** | **205** | **59.93** | **ID/SO** | **205** | **60.26** | **ID/SO** |
| **147** | **52.39** | **ID/DU/SO** | **147** | **51.39** | **ID/DU/SO** | **147** | **52.81** | **ID/DU/SO** | **147** | **53.51** | **ID/DU/SO** |
| 102.9 | 36.31 | ID/DU/SO | 102.9 | 34.74 | ID/DU/SO | 102.9 | 36.34 | ID/DU/SO | 102.9 | 36.5 | ID/DU/SO |
| 307.1 | 23.56 | ID/SO | 307.2 | 20.09 | ID/SO | 307.1 | 23.7 | ID/SO | 307.1 | 24.24 | ID/SO |
| 320.2 | 18.98 | ID/SO | 320.2 | 17.02 | ID/DU | 320.2 | 19.67 | ID/SO | 320.2 | 19.6 | ID/SO |
| 218.1 | 14.17 | ID/DU/SO | 218.1 | 12.52 | ID/DU/SO | 218.1 | 14.24 | ID/DU/SO | 218.1 | 14.35 | ID/DU/SO |
| 116.9 | 12.82 | ID/DU/SO | 116.9 | 11.97 | ID/DU/SO | 116.9 | 13.01 | ID/DU/SO | 116.9 | 12.84 | ID/DU/SO |
| 206.1 | 11.38 | ID/DU/SO | 206.1 | 12 | ID/DU/SO | 206.1 | 11.58 | ID/DU/SO | 206.1 | 11.42 | ID/DU/SO |
| 204 | 11.66 | ID/DU/SO | 204 | 12.06 | ID/DU/SO | 204 | 12.14 | ID/DU/SO | 204 | 12.29 | ID/DU/SO |
| 321.1 | 8.95 | ID/DU/SO | 321.1 | 9.35 | ID/DU/SO | 321.2 | 9.39 | ID/DU/SO | 321.2 | 9.53 | ID/DU/SO |
| 74 | 8.26 | ID/DU/SO | 74 | 8.67 | ID/DU/SO | 74 | 8.37 | ID/DU/SO | 74 | 8.17 | ID/DU/SO |
| 148 | 7.58 | ID/DU/SO | 148 | 7.39 | ID/DU/SO | 148 | 7.75 | ID/DU/SO | 148 | 8.14 | ID/DU/SO |
| 191 | 8.52 | ID/DU/SO | 191 | 7.78 | ID/DU/SO | 191 | 8.6 | ID/DU/SO | 191 | 8.89 | ID/DU/SO |
| 189 | 8.71 | ID/DU/SO | 189 | 7.71 | ID/DU/SO | 189 | 8.7 | ID/DU/SO | 189 | 8.97 | ID/DU/SO |
| 132.9 | 7.13 | ID/DU/SO | 132.9 | 6.86 | ID/DU/SO | 132.9 | 7.5 | ID/DU/SO | 132.9 | 7.21 | ID/DU/SO |
| 128.9 | 7.21 | ID/DU/SO | 129 | 7.13 | ID/DU/SO | 128.9 | 7.29 | ID/DU/SO | 129 | 7.29 | ID/DU/SO |

Table S4/3: Overview of the GC/MS (Gas chromatography / Mass spectrometry) output for selected standards: Iditol (ID), Dulcitol (DU), Sorbitol (SO) and for eight randomly chosen samples across all species and light environments. Mass to charge ratio (m/z), relative intensity of the base peak (intensity). If intensity is ≥50% (**bold**) the absolute tolerance (**abs**) is ± 10%. If intensity is <50% and ≥25% the relative tolerance (rel) is ±15% (see text for further details).

| ***Shorea argentifolia*** | | **Dark-Light** | ***Shorea leprosula*** | | **Dark-Dark** | ***Shorea leprosula*** | | **Dark-Light** | ***Shorea argentifolia*** | | **Dark-Light** |
|---|---|---|---|---|---|---|---|---|---|---|---|
| m/z | intensity | range | m/z | intensity | range | m/z | intensity | range | m/z | intensity | range |
| **217** | **71.25** | **ID** | **217** | **72.13** | **ID** | **217** | **69.96** | **ID** | **217** | **72.76** | **ID** |
| **319.1** | **70.21** | **ID** | **319.1** | **72.84** | **ID** | **319.1** | **68.92** | **ID** | **319.1** | **73.62** | **ID/SO** |
| **205** | **58.78** | **ID/SO** | **205** | **59.76** | **ID/SO** | **205** | **57.91** | **ID/SO** | **205** | **60.46** | **ID/SO** |
| **147** | **51.98** | **ID/DU/SO** | **147** | **53.02** | **ID/DU/SO** | **147** | **51.87** | **ID/DU/SO** | **147** | **52.42** | **ISD/DU/SO** |
| 102.9 | 36.3 | ID/DU/SO | 102.9 | 36.29 | ID/DU/SO | 102.9 | 34.78 | ID/DU/SO | 102.9 | 36.76 | ISD/DU/SO |
| 307.1 | 23.57 | ID/SO | 307.1 | 23.79 | ID/SO | 307.1 | 22.76 | ID/SO | 307.1 | 24.66 | ID/SO |
| 320.2 | 18.92 | ID/SO | 320.2 | 19.26 | ID/SO | 320.2 | 19.2 | ID/SO | 320.2 | 19.56 | ID/SO |
| 218.1 | 13.73 | ID/DU/SO | 218.1 | 13.93 | ID/DU/SO | 218.1 | 13.77 | ID/DU/SO | 218.1 | 13.63 | ISD/DU/SO |
| 116.9 | 13.31 | ID/DU/SO | 116.9 | 12.94 | ID/DU/SO | 116.9 | 12.34 | ID/DU/SO | 116.9 | 12.99 | ISD/DU/SO |
| 206.1 | 11.25 | ID/DU/SO | 206.1 | 11.62 | ID/DU/SO | 206.1 | 11.33 | ID/DU/SO | 206.1 | 11.62 | ISD/DU/SO |
| 204 | 12.08 | ID/DU/SO | 204 | 12.07 | ID/DU/SO | 204 | 11.04 | ID/DU/SO | 204 | 12.04 | ISD/DU/SO |
| 321.2 | 9.1 | ID/DU/SO | 321.2 | 9.25 | ID/DU/SO | 321.1 | 8.81 | ID/DU/SO | 321.2 | 9.3 | ISD/DU/SO |
| 74 | 8.28 | ID/DU/SO | 74 | 8.38 | ID/DU/SO | 74 | 8.42 | ID/DU/SO | 74 | 8.28 | ISD/DU/SO |
| 148 | 8.07 | ID/DU/SO | 148 | 7.76 | ID/DU/SO | 148 | 7.76 | ID/DU/SO | 148 | 7.93 | ISD/DU/SO |
| 191 | 8.73 | ID/DU/SO | 191 | 8.62 | ID/DU/SO | 191 | 8.5 | ID/DU/SO | 191 | 8.43 | ISD/DU/SO |
| 189 | 8.2 | ID/DU/SO | 189 | 8.86 | ID/DU/SO | 189 | 8.38 | ID/DU/SO | 189 | 8.6 | ISD/DU/SO |
| 132.9 | 7.27 | ID/DU/SO | 132.9 | 7.17 | ID/DU/SO | 132.9 | 6.83 | ID/DU/SO | 132.9 | 7.38 | ISD/DU/SO |
| 129 | 7.23 | ID/DU/SO | 129 | 7.33 | ID/DU/SO | 129 | 6.97 | ID/DU/SO | 129 | 7.26 | ISD/DU/SO |

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# 8 Chapter Five

## 8.1 Effects of Ectomycorrhiza on Seedling Growth Across a Range of Forest Floor Light Conditions

*(with C. Philipson, R.C. Ong, N. Majalap, S. Egli, A. Hector, manuscript)*

## 8.2 Abstract

A shadehouse experiment was applied to test for the effect of light, fertilization and ectomycorrhizal inoculation on the growth of *Vatica albiramis* van Slooten (Dipterocarpaceae) seedlings. We hypothesised that it is more advantageous to plants to trade carbon for nutrients with ectomycorrhiza under low light than hight light. We tested this by relating the ectomycorrhizal benefit to the plant with an increase in relative mass growth, where growth is predicted to increase when light conditions and therefore carbohydrate supply is higher. Light conditions simulated the forest understorey (Dark; 3%), a small gap (Medium; 11%) and a large gap (Light; 33% full sunlight) and applied a fully-factorial combination of fertilizer (F-/+) and ectomycorrhiza (ECM-/+) treatments within light conditions. We expected that seedling growth in the dark condition correlates negatively with ectomycorrhizal root tips, because plants should allocate the limited carbohydrates to either growth or the support of ectomycorrhiza. The results rejected our hypothesis as the relationship between seedling growth and the proportion of ectomycorrhizal root tips was significantly positive across all light conditions. The method of soil sterilization by sun heat used in this study significantly lowered relative growth in nursery seedlings over one year. We propose an "easy to use" method to significantly increase ectomycorrhizal association that can be applied in remote large scale forest rehabilitation projects.

**Keywords**

*Vatica albiramis*, dipterocarp, Borneo, ectomycorrhiza, soil solarisation

## 8.3 Introduction

The exploitation of tropical forests for timber in Malaysian Borneo has severely degraded the condition of this fragile ecosystem since the 1980s (Marsh and Greer, 1992). Rising awareness that degraded forest can be restocked with native timber trees resulted in active research on forest rehabilitation during the 1990s

(Appanah, 2001). In North Borneo members of the Dipterocarpaceae family are predominantly used for forest rehabilitation due to their ecological and economic importance (Romell et al., 2008, Ashton, 1982, Symington, 1943). External factors that affect dipterocarp seedling growth and survival in logged forests were identified as soil compaction along log landings and skid trails (Nussbaum et al., 1996), reduced light levels due to intervening vegetation (Bebber et al., 2002), nutrient limitation due to topsoil disturbance (Nussbaum et al., 1995) and inadequate ectomycorrhizal formation (Turner et al., 1993, Lee et al., 1995). As a result a number of studies addressed the importance of the ectomycorrhiza association on dipterocarps in line with efforts to plant native trees into logged forest (Lee and Alexander, 1994). Seedlings grown in full polybags under nursery conditions are raised from collected seeds or wildings and are known to also depend on light, nutrients, ectomycorrhiza for successful growth. Both light and nutrients, in particular phosphorus, are a limiting resource for dipterocarp seedling growth in the understorey of tropical forests in Borneo (Brearley et al., 2007). Studies from an artificial shadehouse experiment and a field study on *Hopea odorata* (Dipterocarpaceae) showed a positive correlation between light and nutrient supply (Kamaluddin and Grace, 1996, Raja Barizan, 1996). Ectomycorrhizal fungi were shown to be beneficial for dipterocarp growth because they possess the ability to break down the structure of plant litter and absorb N and P from plant polymers (Selosse et al., 2006). In return the fungi receives sugars and vitamins from the host-plant. The combined positive effect of nutrient availability and ectomycorrhizal infection on dipterocarp seedling growth was documented in pot studies with seedlings of *Dryobalanops lanceolata, Hopea nervosa* and *Parashorea tomentella* (Lee and Alexander, 1994, Brearley, 2003). To our knowledge, only one study has tested for the combined effects of light, nutrients and ectomycorrhiza on dipterocarp (*Shorea leprosula* and *Hopea nervosa*) growth (Brearley et al., 2007). We tested whether light, fertilisation, controlled ectomycorrhizal inoculation and their interaction affected the growth of *Vatica albiramis* van Slooten seedlings in a controlled experiment.

### 8.3.1 Ecological hypothesis

We expected that forest floor light conditions influence carbon fixation and may therefore alter the potential value of carbohydrates to the plant. Assuming non-limiting nutrient and water supply in high light conditions, the carbon fixation through the process of photosynthesis is expected to be high and the relative value of carbon to the plant is low. In contrast under limiting nutrient supply and in low light conditions, the carbon fixation was predicted to be low and the relative value of carbon to the plant was predicted to be higher. We therefore hypothesised that it is more advantageous to plants to trade carbon for nutrients with ectomycorrhiza under low light than hight light. We tested this by relating the ectomycorrhizal benefit to the plant with an increase in relative mass growth, whereby we expected that the growth is higher when light conditions and carbohydrate supply is higher.

### 8.3.2 Applications

Careful soil treatment may be crucial for the establishment and resistance of the seedling stock and for a later success of the replanting effort. However, uncareful soil treatment is widespread in nurseries after the soil has been excavated in the field (pers. observ.). Nursery seedlings are generally planted into shredded soil. Due to the high clay content the soil is normally sun dried for at least one week prior to shredding. Drying and heating of the soil may alter the soil texture but also kill existing hyphae and spores of ectomycorrhizal fungi (soil solarisation). To what extent soil solarisation reduces the benefits of associated ectomycorrhiza on seedling growth is not well understood for dipterocarps raised under nursery conditions. We were therefore interested to test whether initial soil treatment may alter subsequent seedling growth. We present an “easy to use” method to significantly increase ectomycorrhizal association that can be applied in remote large scale forest rehabilitation projects.

## 8.4 Material and Methods

### 8.4.1 Experimental set-up

Our study site (N05º05'20" E117º38'32", 102 m.a.s.l.) was located in the Malua Forest Reserve in the eastern part of the state of Sabah in Malaysian northern Borneo. The shadehouse experiment was situated in logged lowland mixed dipterocarp forest that is aseasonal with an annual rainfall of approximately 3000 mm during the measurement period (Chapter 1). A total of fifteen shade houses (4 x 6 x 5 m) were aligned in five blocks of three shadehouses, randomly allocated to one of 3 light levels (see below). In order to minimise self shading blocks were sited along an east-west line with 3 m space between the houses and >10 meters between blocks. Within shadehouses, seedlings were spaced 0.3 m apart. To reduce the effect of herbivory, pots were located 0.3 m above ground and wire mesh protected the seedlings from mammal damage.

We simulated three light environments by using a triple, a double and a single layer of 70% black shade cloth: the forest understorey (Dark; 3% full sunlight), a small gap (Medium; 11% full sunlight) and a large gap (Light; 33% full sunlight). Seeds were randomly allocated to the shadehouses and to one of the four treatments (F-/ECM-, F-/ECM+, F+/ECM-, F+/ECM+), representing a fully-factorial design. Seeds were either fertilized (F+) or not (F-) and either innoculated with ectomycorrhiza (ECM+) or not (ECM-). Environmental measures were taken inside all shadehouses for one day each (12th - 26th July 2007) between 08:00 and 16:00 with a data logger (Lynx data hog, Skye, USA). The data logger was set to record measurements from photosynthetic active radiation (PAR), red light, far red light, relative humidity and temperature sensors every 30 seconds and record average values every 10 minutes (Table 8). Light readings outside were collected every hour with a quantum sensor (LI-189, LiCor, USA) to calculate relative light availability inside the shadehouses. Light sensors inside the shadehouse and outside (Skye Quantum and LiCor LI-189) were calibrated before measuring by comparing mean per hour over a full day.

Table 8 Comparison of mean environmental conditions (±SEM) within the shade houses. PAR* is reported as the percentage of outside light conditions.

| | Unit | Dark | Middle | Light |
|---|---|---|---|---|
| PAR* | % | 2.6 ± 0.6 | 10.8 ± 1.3 | 32.9 ± 4.5 |
| PAR | µmol s-1 m-2 | 11.7 ± 2.3 | 42.9 ± 4.9 | 127.5 ± 13.2 |
| Red / Far Red | Ratio | 0.92 ± 0.08 | 0.87 ± 0.04 | 0.85 ± 0.06 |
| Relative Humidity | % | 81.3 ± 2.5 | 80.1 ± 0.6 | 80.9 ± 2.4 |
| Temperature | °C | 27.3 ± 0.6 | 27.3 ± 0.2 | 27.0 ± 0.5 |

### 8.4.2 Seed material

The choice of the experimental species was determined by seed availability, since dipterocarps fruit irregularly and seeds germinate quickly after desiccation under moist and warm conditions (Appanah and Turnbull, 1998). *Vatica albiramis* (local name resak puteh) belongs to the vernacular group of resak, a heavy hardwood (880-990 kg $m^{-3}$ at 15% moisture content). Besides its importance for timber it is also known for its use as a non-timber forest product. The Dayak people of central Kalimantan use an extract of *Vatica albiramis* as a pest and disease protection during rice cultivation (Limin et al., 2007). No published work on seedlings for this particular species could be found, however to our knowledge two studies exist on the regeneration of *Vatica hainanensis* from Hainan Island, China (Yujia, 1996) and *Vatica oblongifolia* from Sabah, Malaysia (Scholes et al., 1997).

Seeds of two *Vatica albiramis* trees were collected directly from the branch to ensure that seedlings would not be ectomycorrhizal prior to experimental start. Seeds were numbered individually, weighed and germinated in sterilised plastic boxes to test for viability prior to planting (n = 776). Germination started after one week and lasted for 19 days in total. 489 (63%) seeds germinated and a random selection thereof was used for the experiment. 287 did not germinate, whereby both seed weight and tree identity determined germination rates (unpubl. data). We randomly allocated the seeds to the treatments using the sample function in R (R Development Core Team, 2009).

### 8.4.3 Soil source

The sub-soil used is classified as orthic acrisol, which is acidic (pH = 5), highly weathered, with poor nutrient availability (total nitrogen: 0.06%, total phosphorous: 31.7 µg $g^{-1}$, extractable potassium: 0.19 milliequivalents per 100 g soil, base saturation: 80.9%). Sub-soil was shredded, then solarised twice for three days consecutively under black plastic (>60° C) following the method described in (Yasman 1995). Shredded sub-soil treated similarly is readily used in nurseries to raise seedling stocks for forest rehabilitation efforts. We ensured that the soil remained in wet condition at all times to prevent altered soil structure. River sand was sterilised by heating with sufficient water in half a barrell for approximately 30 minutes over a fire. Sterile soil was then mixed with sterile river sand (ratio 2:1) for easier excavation of the root system and associated ectomycorrhiza. Viable seeds were directly planted into black polyethylene bags (0.2 x 0.3 m) filled with the sterile soil and sand mixture.

### 8.4.4 Mycorrhizal inoculation and fertilization

Slow release fertiliser (1.25 g NPK, Osmocot, USA) was added to F+ treatments at the start of the experiment and subsequently at every harvest (Table 9). ECM+ treatments were inoculated with a 2:1 mixture of forest litter (collected under the mother tree) and ectomycorrhizal infected nursery soil from seedlings of the same species. The inoculum was kept wet for 10 days, then diluted with water and mixed thoroughly. 3.5 dl of the litter and soil inoculum were poured onto the germinated ECM+ seedlings to ensure high infection levels. Efforts were taken to minimize the natural infection with ectomycorrhiza of the untreated seedlings (ECM-). In particular we reduced the spraying with water between treatments to minimize water droplets and we touched the soil as little as possible. No fungicide treatment was applied to control for ectomycorrhizal infection. Seedlings were watered regularly and relocated twice within the shadehouses to avoid drought and positioning effects.

Table 9 Soil analysis (mean ± SEM) of unfertilised (F-) and fertilised (F+) across all light conditions for the first harvest (day 143). N: Nitrogen, P: Phosphorous, Exctractable K: Kalium, Mg: Magnesium, Ca: Calcium, Mn: Mangan (m-equiv. $100g^{-1}$:, milliequivalents per 100g soil), ECEC: Effective cation exchange capacity, Bsat: Base saturation (for definitions and methods see text).

| | Unit | F- (n = 3) | F+ (n = 3) |
|---|---|---|---|
| pH | $H_2O$ | 5.1 ± 0.1 | 4.6 ± 0.1 |
| Total N | % | 0.06 ± 0.01 | 0.07 ± 0.01 |
| Total P | $\mu g\ g^{-1}$ | 22.6 ± 2.6 | 59.3 ± 22.9 |
| Extractable K | m-equiv. $100g^{-1}$ | 0.16 ± 0.01 | 0.42 ± 0.12 |
| Extractable Mg | m-equiv. $100g^{-1}$ | 2.6 ± 0.1 | 2.5 ± 0.1 |
| Extractable Ca | m-equiv. $100g^{-1}$ | 7.5 ± 0.5 | 7.2 ± 0.3 |
| Extractable Mn | m-equiv. $100g^{-1}$ | 0.03 ± 0.01 | 0.05 ± 0.01 |
| ECEC | m-equiv. $100g^{-1}$ | 12.7 ± 0.4 | 12.8 ± 0.3 |
| Bsat | % | 81.3 ± 2.1 | 79.0 ± 2.3 |

### 8.4.5 Experimental phase

The experiment started on the 21st of July 2006. Full replications of the experimental design (n = 60) were harvested 143 days, 283 days and 410 days after the experiment started. At each harvest we washed the soil and sand mixture carefully off the roots and randomly selected five roots of the entire root system. We counted the presence of ectomycorrhiza on 200 root tips of every seedling to estimate the percentage of ectomycorrhizal infection and the associated morphotypes following the description of Agerer and Rambold (2004-2007) (Table S5). Leaves, shoots and roots of the seedlings were separated, oven dried to a constant weight (72 h, 65 °C) and individually measured.

### 8.4.6 Soil analysis

Soil samples of six randomly selected fertilised and unfertilised pots were collected at the first harvest and analysed for nutrient content (Table 9). Air-dried samples were ground to pass through a 2-mm sieve and analysed for pH, total N and P, extractable K, Mg, Ca, Mn and effective cation exchange capacity (ECEC)

(detailed protocols in Majalap and Chu (1992)). The pH was measured with a combination glass-calomel electrode (pH Meter Model 140, Corning, UK) in a 1:2.5 ratio of soil to destilled water suspension. Total N was determined following the Kjeldahl digestion described by Bremner (1965) on a block digestor and the digest measured for nitrogen content (SFA2 autoanalyser, Burkard, UK). Extraction of soil available P followed the method of Bray and Kurtz (1945) and the P content in the extract was measured as described in (Anderson and Ingram, 1993). For the determination of K, Mg, Ca, Mn the soil was leached with 1M ammonium acetate (Gillman et al., 1983) and the leachate analysed for each element on an atomic absorption spectrophotometer (GBC 932, GBC Scientific Equipment Pvt. Ltd., Australia).

### 8.4.7 Methods check for inoculation

At the first harvest, seedlings that were inoculated with ectomycorrhiza were found to have increased levels of ectomycorrhizal infected root tips for the medium and the light condition in the unfertilized (F-/ECM+; 27-28% increase) and fertilized treatments (F+/ECM+; 28-33% increase). This confirmed that the soil solarization and the inoculation treatment worked and that treatment effects can be measured for up to five months without the addition of fungicide (Fig.20). Analysis of soil fertility for the first harvest revealed that soil pH was slightly more acidic in the fertilizer treatments (Table 9). Further we detected differences between unfertilised and fertilised soil in total P and extractable K. All other measures of nutrient availability, including total N concentration were similar between treatment levels.

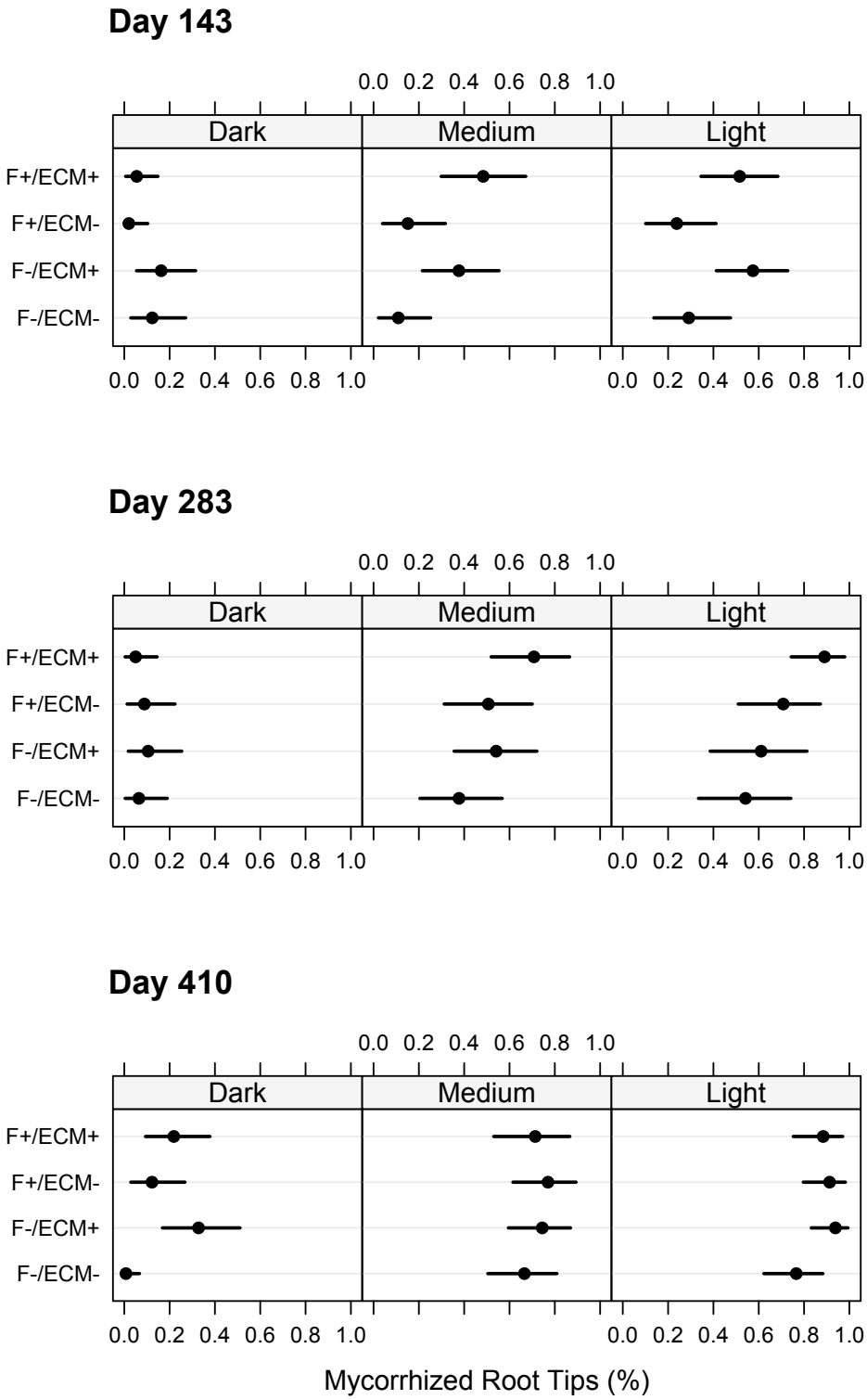



Figure 20 Inoculation (Mean ± SEM) significantly increased proportion of mycorrhizal root tips in medium and high light, but not in the dark of the first harvest (day 143). For the second (day 283) and third harvest (day 410) the treatment effect could not be observed (except for the dark of the third harvest). Light conditions: 3% (Dark), 11% (Medium) and 33% full sunlight (Light). Note that the nutrient treatments were pooled: ECM+ inoculated with ectomycorrhiza (F+/ECM+ and F-/ECM+); ECM- not inoculated (F-/ECM- and F+/ECM-).

### 8.4.8 Statistical analysis

All analysis and graphical presentation was performed in R (R Development Core Team, 2009). We used the *lme* function (Pinheiro and Bates 2000) implemented in the *nlme* package for R 2.9.0 since our experimental design included fixed and random effects. Light conditions (Dark, Medium, Light), fertilizer (F-, F+) and ectomycorrhiza (ECM-, ECM+) were treated as fixed effects. Block (n = 5) and shadehouses (n = 15) were treated as random terms. We checked for normally distributed residual errors prior to analysis. Mycorrhizal root tips (%) were arcsin square root transformed for analysis and back transformed for ease of interpretation. Initial size-corrected average relative growth rate (RGR; g $g^{-1}$ $day^{-1}$) was calculated on the assumption that a higher seedling mass growth reflects a higher overall plant fitness (Hunt, 1990):

$$RGR = \frac{\log_e W_2 - \log_e W_1}{T_2 - T_1} \qquad (9)$$

RGR is calculated as change in log mass divided by the time interval ($T_2$-$T_1$). Relative growth examines growth on a percentage basis, taking the logarithm of the mass is based on the assumption that the seedlings grow at a constant exponential rate (Philipson, 2009). Initial size-corrected average relative growth rate (RGR) corrected for differences in initial seed mass was used as a surrogate for individual seedling performance under the different treatment levels (Nicieza and Alvarez, 2009). However, because this study examines a single species, rather than multiple species where initial sizes may be biased with species, the starting sizes of the treatments were not considered to be different as the variation was small (Table 10). Seed mass was derived with an allometry ($R^2$ = 0.9, y = -0.04 + 0.56x) from a selection of dried seeds (n = 34, 72 h, 65° C).

Presence or absence of morphotypes and diversity of morphotypes where fungi were present was analysed with a generalised linear mixed effect model using the *glmmPQL* function from the *MASS* package

(Venables and Ripley, 2003). Model checking was performed with the *binnedplot* function of the *arm* library (Gelman et al., 2009) for the binomial model.

Table 10 Comparison of initial seed mass (in gram: Mean ± SEM) at experimental start. Note the similarity in size ranges between plants and treatments: F: Fertilizer, ECM: Ectomycorrhiza inoculation, Light conditions: Dark, Medium, Light.

| | Dark | Medium | Light |
|---|---|---|---|
| F - / ECM - | 0.75 ± 0.03 | 0.71 ± 0.03 | 0.73 ± 0.05 |
| F - / ECM + | 0.77 ± 0.07 | 0.68 ± 0.04 | 0.73 ± 0.05 |
| F+ / ECM - | 0.77 ± 0.03 | 0.74 ± 0.05 | 0.74 ± 0.05 |
| F + / ECM + | 0.63 ± 0.05 | 0.77 ± 0.05 | 0.71 ± 0.5 |

## 8.5 Results

We hypothesised that it is more advantageous to plants to trade carbon for nutrients with ectomycorrhiza under low light than hight light. We expected to find a negative relationship between seedling growth and the proportion of ectomycorrhizal root tips in the dark. In light conditions we expected the relationship to be positive. In contrast to our expectations the relationship did not vary across light conditions and was positive across the range of forest floor light conditions (Mean slope of 0.0062 g $g^{-1}$ $day^{-1}$; with 95% CI = 0.0053 to 0.0072) (Fig.21; overall $R^2$ = .59)).

### 8.5.1 Seedling growth

Throughout all three harvests mean relative growth of seedling mass (g $g^{-1}$ $day^{-1}$) was strongly affected by light conditions (Fig.22). For the final harvest seedlings grew significantly better in the medium than in the dark (Mean difference of -0.0041 g $g^{-1}$ $day^{-1}$; with 95% CI = -0.0024 to -0.0006) but significantly worse than in the light (Mean difference of 0.0026 g $g^{-1}$ $day^{-1}$; with 95% CI = 0.0008 to 0.0043) (Fig.22, day 410). None of the applied treatments (fertilizer, ectomycorrhiza) significantly altered seedling growth

in the dark, suggesting that seedlings were close to their light compensation point. However, we did find a significant positive effect of fertilization on seedling mass growth in medium (Mean difference of 0.0017 g $g^{-1}$ $day^{-1}$; with 95% CI = 0.0003 to 0.0032) and light conditions (Mean difference of 0.0025 g $g^{-1}$ $day^{-1}$; with 95% CI = 0.001 to 0.0039). In contrast inoculation with ectomycorrhiza did not cause an increased growth in either the medium or the light conditions. According to our results the combined effect of fertilizer and ectomycorrhiza (F+/ECM+) responded differently according to the light environment. Whereas we did not observe a significant increase in growth compared to fertilised seedlings (F+/ECM-) in the medium, such an effect was significant for the light condition (Mean difference of -0.0018 g $g^{-1}$ $day^{-1}$; with 95% CI = -0.0033 to -0.0004).

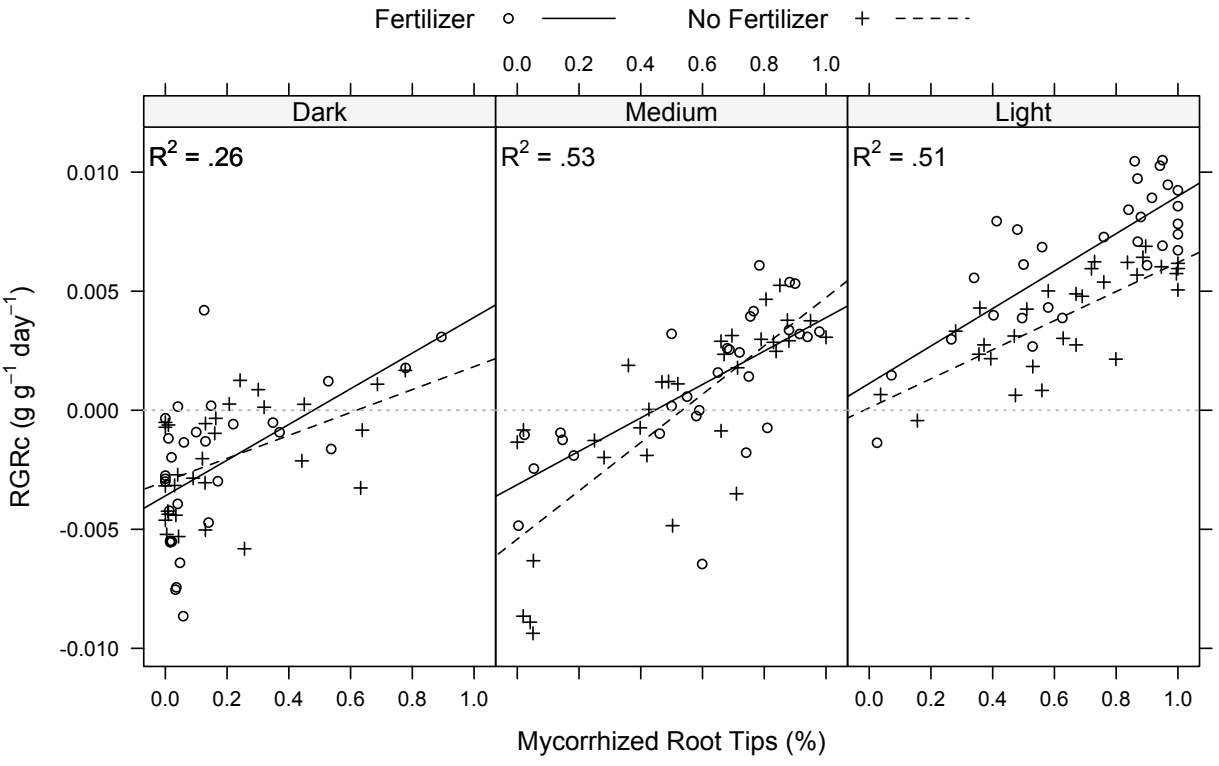



Figure 21 Relationship between initial size-corrected relative growth rate ($RGR_c$) of total seedling mass and percentage of mycorrhized root tips. Light conditions: 3% (Dark), 11% (Medium) and 33% full sunlight (Light). Adjusted $R^2$ are shown for each light treatment separately (overall $R^2$ = .59).

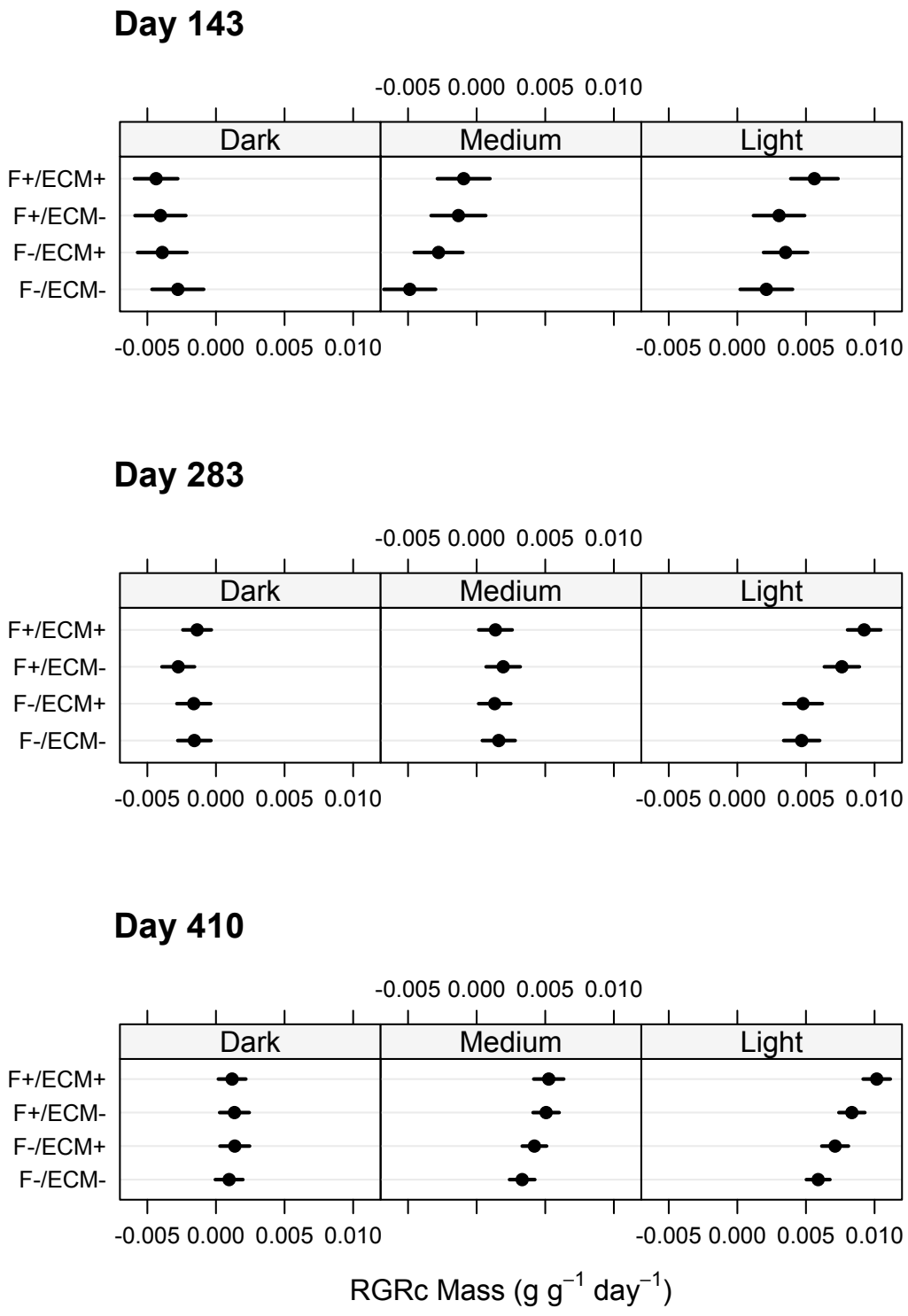



Figure 22 Initial size corrected relative growth rate (RGRc; Mean ± SEM) increases across the light conditions, over time (first (day 143), second (day 283) and third harvest (day 410)) and treatments (i.e. ECM+ and F+ treatments are sometimes additive). The growth increase is evident in particular for the third harvest (day 410) in the light treatment. Light conditions: 3% (Dark), 17% (Medium) and 30% full sunlight (Light). Treatments: F-/ECM- (control treatment); F-/ECM+ (ectomycorrhiza added); F+/ECM- (nutrient added); F+/ECM+ (ectomycorrhiza and nutrient added).

### 8.5.2 Mycorrhizal morphotypes

In total we counted nine seedlings without mycorrhizal morphotypes across all three harvests (n = 8 in the dark treatment, n = 1 in the medium treatment). As expected, most seedlings without morphotypes were found in the untreated control (F-/ECM-; n = 5), followed by the fertilised treatments (F+/ECM-; n = 2 and F+/ECM+; n = 2). Across all harvests we did not detect a difference in morphotype presence or absence with regard to treatment levels (light, fertilisation) (Table S6). In contrast to our expectations, we detected morphotype differences in the presence or absence between fertilisation levels only for one morphotype (L). This suggests that the fertilization was not high enough to significantly alter morphotype presence. Interestingly, despite the reduced levels of ectomycorrhizal association in the dark, morphotype presence was similar (10-11 morphotypes) to the medium and the high light conditions (12-14 morphotypes) (Table S6). In contrast, we did find altered levels of morphotype abundance (number of morphotypes on a given seedling) where fungi were present for the medium treatment of the first harvest. More morphotypes were present on inoculated seedlings of unfertilized (F-/ECM+; Mean difference of 2.4 morphotypes; with 95% CI = 1.3 to 4.2) and fertilized seedlings (F+/ECM+; Mean difference of 1.7 morphotypes; with 95% CI = 1.1 to 2.7) compared to the controls (F-/ECM- and F+/ECM-). The difference could not be found for the dark or the light conditions and disappeared for the subsequent harvests.

## 8.6 Discussion

As reported in previous studies (Becker, 1983, Yasman, 1995, Ingleby et al., 1998) we found a positive correlation ($R^2$>.59) of relative mass growth and ectomycorrhizal infected root tips across all three light conditions (Fig.21). We can therefore reject our hypothesis that it is more advantageous to seedlings to trade carbon for nutrients with ectomycorrhiza under low compared to high light conditions. In addition our results suggest that even small increases in growth rates over time may alter percentage of ectomy-

corrhizal root tips. Seedlings growing in the dark acquired only low ectomycorrhizal associations after four months (2-16%) after which the level of infection gradually increased for the second (21-26%) and the third harvest (24-70%). This increase was most likely related to an increase in seedling mass growth which switched from negative to positive between the second and the third harvest (Fig.22, day 283 to day 410). Our results therefore indicate that the low light conditions (11.7 ± 2.3 µmol $s^{-1}$ $m^{-2}$ SEM) may not have been dark enough to keep seedlings below the light compensation point which is reported at 6-8 µmol $m^{-2}$ $s^{-1}$ for dipterocarps (Eschenbach et al., 1998). However such conditions would be necessary to test whether the mutualistic association between ectomycorrhiza and dipterocarps becomes negative and if initial mass loss or delayed mass growth may be caused by associated ectomycorrhiza (Bever, 2002).

In contrast to other studies we found that an increase in seedling mass growth was related to quantity of mycorrhiza (percentage of mycorrhizal root tips) but not related to the abundance of the individual morphotypes (Brearley et al., 2007). Brearley et al. (2007) further reported that their hardwood species (*Hopea nervosa*) did not show altered growth rates in relation to P fertilization when grown in shade-chambers. In contrast, the light hardwood species (*Shorea leprosula*) responded to P fertilization with an increased growth rate and increased foliar P concentrations. Results from our study may confirm their findings of the hardwood species, since increased levels of total P and extractable K but not of total N in the fertilization treatments suggest that N was the limiting resource (Burslem et al., 1995, Bungard et al., 2000, Brearley et al., 2005). In our study the response to nutrient addition varied according to the exposed light condition and no response could be found in understorey light conditions as suggested by Nussbaum et al. (1995). As expected, fertilized seedlings (F+) did show reduced levels of ectomycorrhizal root tips, even though the finding was a mere trend and more advanced methods of soil sterilization are necessary to study the relation between fertilization and ectomycorrhizal infection (Johnson, 1993).

Daily watering of the soil and sand mixture may have led to rapid nutrient depletion, which could explain why ectomycorrhiza inoculation without fertiliser (F-/ECM+) was not beneficial for seedling growth over all light treatments and harvests. If nutrient levels are too low the beneficial effect of the ectomycorrhizal association may therefore disappear. However, seedlings (F-/ECM+) did show a mean increase in mycorrhizal root tips with increasing light conditions and over time indicating that despite low nutrient levels ectomycorrhiza remained associated with the host-plant.

We showed that our adapted method of initial soil solarisation significantly reduced ectomycorrhizal infection for up to five months without the addition of fungicide treatment. The effect could be measured for over one year, even though the evidence of the inoculation treatment disappeared after five months, since root tips of all seedlings were colonised by then. This suggests that the combined effects of early levels of mycorrhizal associations and nutrient availability are beneficial for nutrient use efficiency of *Vatica albiramis* seedlings over the long term. However, at the first harvest seedlings without inoculation still had about 15% of uncontrolled infection in the medium treatment and 30% in the high light treatment. Further, both inoculated and non-inoculated seedlings of the dark treatment had similar percentages of ectomycorrhizal root tips (16% and 12% respectively). Remnants of fungal hyphae and spores after soil solarization, water- and airborne fungal spores may explain these similar abundances.

Our approach of using a 2:1 mixture of forest litter and nursery soil indicates that such crude approaches can already lead to beneficial effects, without the addition of commercially available ectomycorrhiza strains. In remote locations, where logistic support is limited this method could be applied to improve the ectomycorrhizal associations and subsequent growth increase in nursery seedlings. However, one should consider other species of dipterocarps, in particular light hardwoods, to derive general conclusions since dipterocarps are known to show a great range of adaptability to changes in biotic and abiotic conditions (Scholes et al., 1997). The adaptability in seedling performance may also be related to other factors, such

as the diversity and the abundance of related ectomycorrhizal strains which could not be directly tested in this study (Turjaman et al., 2006, Brearley et al., 2007). Further, it remains to be tested if our findings significantly alter seedling performance under field conditions. In particular light is known to be highly heterogenous in the understorey of tropical rain forests (Chazdon and Pearcy, 1991, Bungard et al., 2002, Leakey et al., 2004). Sunflecks may compensate for low light conditions if understorey plants can respond to excess light (Watling et al., 1997). Such heterogeneity in light is normally not accounted for in artificial shadehouse experiments and is best simulated in forest gaps (Dalling et al., 1999, Dalling et al., 2004). In contrast responses to high light environments were shown to be comparable between shadehouse- and forest-grown seedlings (Bloor, 2003), suggesting that the results presented here may be of direct relevance for outplanted seedlings in the field.

## 8.7 Conclusion

Effects of ectomycorrhiza on growth of seedlings of a tropical tree and the proportion of ectomycorrhizal root tips were significantly positive across all light conditions. Our results therefore show that *Vatica albiramis* seedlings are associated with ectomycorrhiza across a range of forest floor light conditions, including the dark understorey and a large gap. We therefore reject our hypothesis that it is more advantageous to plants to trade carbon for nutrients with ectomycorrhiza under low light than hight light. Our findings further show that soil solarization significantly lowered ectomycorrhizal association which decreased relative growth of nursery seedlings grown in light conditions over one year. We advise those who dry soil in sun heat prior to planting to support the nursery seedling stock with low nutrient addition and initial ectomycorrhizal inoculation to optimise plant growth in solarized soil.

## 8.8 Acknowledgements

We thank: Martina Peter and Lee Su See for helpful discussion of the experimental design and morphotype identification; Charles Godfray and Glen Reynolds for their efforts in setting up and supporting the Sabah Biodiversity Experiment; Karin Beer together with research assistants from the Malua Field Station for providing field assistance; Jake Snaddon for comments on the manuscript. The Economic Planning Unit Sabah, Malaysia and the Danum Valley Management Committee approved this field study. This project was funded by the University Zurich and is part of the Royal Society South-East Asia Rainforest Research Programme (Project No. RS243). This is paper no. X of the Sabah Biodiversity Experiment.

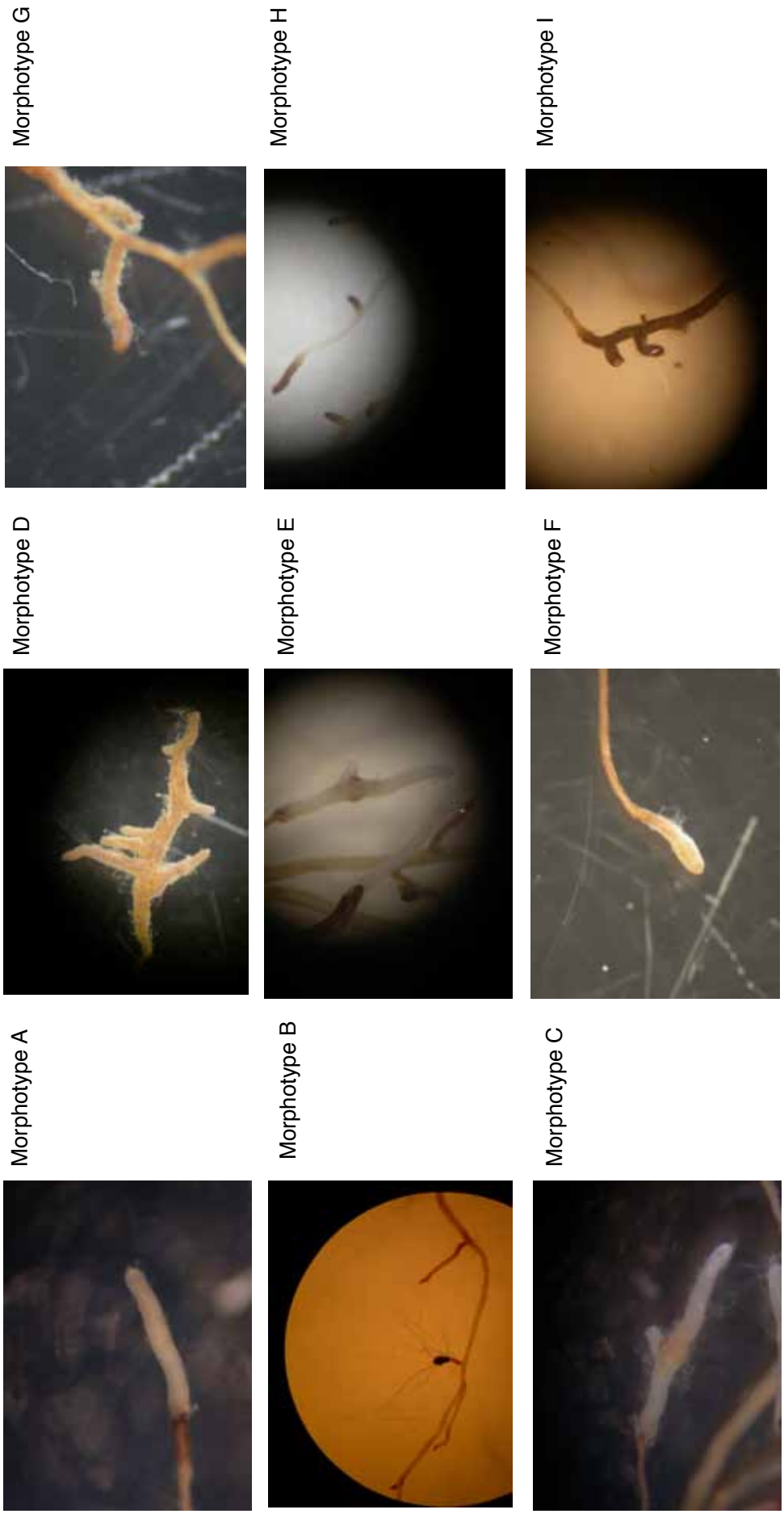
## 8.9 Appendix

Table S5 Ectomycorrhiza morphotypes description, following the method of Agerer and Rambold (2004-2007).

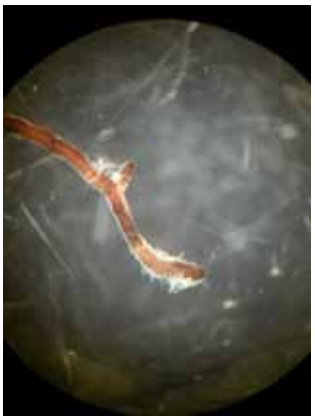
| Morphotype | Color | Ramification | Shape | Surface | Rhizomorphal connection |
|---|---|---|---|---|---|
| A | White /Grey | Simple | Straight | Cottony | Ensheathed / Hairy |
| B | Green / Black | Simple | Straight | Stringy | Growing off in flat angles |
| C | White | Monopodial-Pinnate | Straight | Cottony | Ensheated / Hairy |
| D | White /Grey | Monopodial-Pinnate | Straight | Cottony | NA |
| E | Grey | Simple | Straight | Stringy | Ensheathed / Hairy |
| F | Dark Brown | Simple | Straight | Stringy | Ensheathed / Hairy |
| G | Dark Grey | Simple | Beaded | Stringy | Ensheathed / Hairy |
| H | Brown | Simple | Straight | Smooth | Smooth Margins |
| I | Brown | Simple | Bent | Smooth | Hyphal Fans |
| J | White | Simple | Straight | Cottony | Hyphal Fans |
| L | Dark Grey | Simple | Straight | Smooth | NA |
| M | Dark Brown | Monopodial-Pinnate | Straight | Smooth | Restricted Point |
| N | Brown w/ white tips | Monopodial-Pinnate | Straight | Smooth | Restricted Point |
| O | White | Simple | Straight | Cottony | Ensheathed / Hairy |
| P | White /Grey | Monopodial-Pyramidal | Straight | Cottony | Restricted Point |
| Q | Green / Black | Irregularly-Pinnate | Bent | Smooth | Restricted Point |

Table S6 Overview of morphotype presence (+) or absence ( ) separated by fertilization (F-/F+) and light treatment (Dark, Medium, Light) for the first harvest (day 143). Total: Sum of all present morphotypes.

| Morphotype | F- | | | F+ | | |
|---|---|---|---|---|---|---|
| | Dark | Middle | Light | Dark | Middle | Light |
| **A** | + | + | + | + | + | + |
| **B** | + | + | + | + | + | + |
| **C** | | + | + | | + | + |
| **D** | + | + | + | + | + | + |
| **E** | + | + | + | + | + | + |
| **F** | + | + | + | + | + | + |
| **G** | + | + | + | + | + | + |
| **H** | + | + | + | + | + | + |
| **I** | + | + | + | + | + | + |
| **J** | + | + | + | + | + | + |
| **L** | + | + | + | | | |
| **M** | | | | | | |
| **N** | + | + | + | + | + | + |
| **O** | | + | + | | + | + |
| **P** | | | + | | | + |
| **Q** | | | | | | + |
| **Total** | 11 | 13 | 14 | 10 | 12 | 14 |


Morphotype G
Morphotype H
Morphotype I
Morphotype D
Morphotype E
Morphotype F
Morphotype A
Morphotype B
Morphotype C

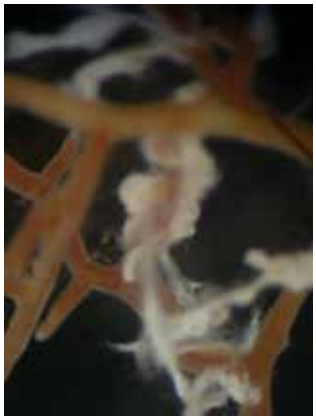
Morphotype Q



Morphotype N

Morphotype O

Morphotype P



Morphotype J

Morphotype L

Morphotype M

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# 9 Chapter Six

## 9.1 No Evidence for the Importance of an Ectomycorrhizal Network for Dipterocarp Seedling Growth

*(with S. Egli, A. Hector, manuscript)*

## 9.2 Abstract

Mycorrhizal networks may be crucial for nurturing juvenile trees that grow in the dark understorey of tropical rainforests. Here we tested for the effect of an ectomycorrhizal network on the regeneration of Dipterocarpaceae. Seedlings of *Dryobalanops lanceolata* and *Shorea parvifolia* were planted in close (2-4 m) and far (15-17 m) proximity of conspecific and heterospecific mature trees in a fully factorial design. We compared height and mass growth of seedlings planted into natural soil with those connected or isolated from to ectomycorrhizal network by polyethylene net of different pore sizes (50 µm, 1 µm). We found no evidence for the benefit of an ectomycorrhizal network on conspecific or heterospecific seedling height and mass growth. Seedlings generally grew better in height and mass when associated with mature *Dryobalanops lanceolata* trees irrespective of the access to the ectomycorrhizal network. Further, seedlings grew better in mass when planted close to mature trees with or without access to the ectomycorrhizal network. These findings suggest that carbon transfer over the soil pathway, but not over the hyphal pathway may be crucial for biomass accumulation of dipterocarp seedlings growing under mature trees.

**Keywords**

Mycorrhizal Network, Dipterocarpaceae, Ectomycorrhiza, tropics, Borneo

## 9.3 Introduction

Positive interaction, also known as facilitation, describes species interactions that benefit at least one of the participants and cause harm to neither (Stachowicz, 2001). Facilitative effects have been shown between young seedlings that grow in the shade of a mature tree and are interconnected through a network of mycorrhizal hyphae in the soil (Selosse et al., 2006). The mycorrhizal network allows nutrient (e.g. nitrogen and phosphorus), carbon and water transfer over the hyphal pathway. This support may be crucial for

nurturing seedlings that grow below the light compensation point and could therefore be an important determinant of forest dynamics (Teste and Simard, 2008).

However, based on field and lab studies Simard et al. (1997) and Simard et al. (1997) concluded that interplant carbon transfer is a complex and variable process that involves hyphal and soil pathway. Here the soil pathway is understood as the absorption by seedlings of soluble sugars from the surrounding soil matrix. Further, all field studies on carbon transfer suffer from the shortcoming that the identity of the pathway (e.g. hyphal pathway or soil pathway) remains unclear (Simard and Durall, 2004). Despite these objections the two published studies from the tropics report a significant effect of a common mycorrhizal network on seedling growth performance and survival (McGuire, 2007, Onguene and Kuyper, 2002). However, there is evidence that mycorrhizal networks in forests may not be the main mechanism for seedling colonisation with ectomycorrhiza (Teste et al., 2009) and may also not provide enough net benefits for seedlings to overcome effects of shade and below-ground competition (Kranabetter, 2005).

Here we tested the importance of the tree-mycorrhiza-seedling connection on seedling height and mass growth of two Dipterocarpaceae species in logged forest of Malaysian Borneo. Dipterocarp seedlings are found to be in high densities close to the parent tree after mast-fruiting events, forming conspecific stands (Blundell and Peart, 2004). Most studies have addressed negative density/distance dependent interactions such as the Janzen-Connell hypothesis to understand mechanisms that drive dipterocarp seedling establishment and tree diversity (Hautier et al., in prep). Hereby, it is suggested that seeds and seedlings of a certain species are less likely to survive when they are close to the parent tree due to increased seed predation and herbivory attack (Blundell and Peart, 1998). To what extend below-ground processes, and in particular a mycorrhizal network may facilitate conspecific seedling establishment is considered to a lesser extent (Allen, 1992). Such findings may be important since ectomycorrhizal networks could explain

why dipterocarp seedlings can persist for several years in the dark understorey and why dipterocarp trees are predominant in tropical forests of South-East Asia.

A number of studies have confirmed that dipterocarp species are obligatory ectomycorrhizal, but may also form endo- and ectendomycorrhizal associations (Singh, 1966, Watling and Lee, 1995, Watling and Lee, 1998, Green and Newbery, 2001, Watling et al., 2002, Kanchanaprayudh et al., 2003, Natarajan et al., 2005, Reddy et al., 2005, Turjaman et al., 2006). It is suggested that the ectomycorrhizal symbiosis evolved early (Ducousso et al., 2004) and is associated with low rates of nutrient and carbon turnover (Alexander and Lee, 2005, Brearley et al., 2005).

The ultimate goal of this study was to experimentally test whether the tree-ectomycorrhiza-seedling connection under low light conditions:

(1) affects the height or mass growth of selected dipterocarp seedlings;

(2) is affected by proximity to the mature tree;

(3) shows altered effects between conspecific and heterospecific tree establishments.

We expected that seedlings which were experimentally excluded from the ectomycorrhizal network would grow less in low light conditions, since they could not benefit from being connected to the surrounding mature trees. This effect was suggested to depend on proximity to the mature tree if the ectomycorrhizal network were to be found within the canopy range of the mature tree only. Further, we expected that the dominance of conspecific stands may have caused a natural selection for supporting seedlings of the same species over others.

## 9.4 Material and Methods

### 9.4.1 Site description

Our study area, the Malua Forest Reserve (N05°05'20" E117°38'32", 102 m.a.s.l.), is located in the Eastern part of the province of Sabah in Malaysian North Borneo. The area is classified as production forest and consists of logged lowland mixed dipterocarp rainforest, the most widespread forest type in equatorial South East Asia. The area is aseasonal with an annual rainfall of ca. 3000 mm during the measurement period (2004-2008) (Chapter 1). The soil in the study area is classified as orthic acrisol, which is acid (pH>5), highly weathered, with poor nutrient availability (81.26% base saturation) and a low organic carbon content (0.36%) (Chapter 1). Bedrock consists of a mixture of mudstone and sandstone areas with miscellaneous rocks (Forestry Department Sabah 2006, unpubl. data). The forest under study was last logged during the early 1980s and has been recovering ever since (Marsh and Greer 1992). Only trees >45 cm DBH were logged, however the understorey seedling bank was heavily disturbed, resulting in forest patches that were dominated by pioneer trees and other, less severely damaged sites which consisted mainly of Non-Pioneer trees (Berry et al., 2008).

In 2000, 500 $ha^{-1}$ of forest, located in the Malua Forest Reserve (approximately 35,000 $ha^{-1}$) was converted into a forest restoration project called the Sabah Biodiversity Experiment. The experiment aims to study the importance of tree species diversity, composition and life history traits for providing fundamental ecosystem services, such as carbon sequestration (Scherer-Lorenzen et al., 2005). Total basal area within the experimental area is 25.0 (± 0.83 SEM) $m^2$ $ha^{-1}$. Dipterocarps are still predominant as a single tree family (6.88 (± 0.17 SEM) $m^2$ $ha^{-1}$), however pioneer trees together, in particular *Macaranga sp.* Muell. Arg. (Euphorbiaceae), *Neolamarkia cadamba* Bosser (Rubiaceae), *Octomeles sumatrana* Miq. (Datiscaceae) and *Duabanga moluccana* Bl. (Sonneratiaceae) occupy a larger area (10.71 (± 0.57 SEM) $m^2$ $ha^{-1}$) (Saner et al., 2009). The focal trees were chosen within a 1.9 $km^2$ area of the Sabah Biodiversity Experiment because

of ongoing logging in the surrounding area during 2007. Ectomycorrhizal associations on dipterocarp roots were shown to respond to logging (Lee et al., 1996, Ingleby et al., 1998) whereby the quantity of root infection was not altered, but fewer species were associated even 40 years post-logging (Watling et al., 1998). Therefore it may not be feasible to test the importance of species composition of the ectomycorrhiza for seedling establishment in the logged area (Cline et al., 2005).

### 9.4.2 Experimental design and species selection

Twenty adult trees belonging to either of two species of Dipterocarpaceae (*Dryobalanops lanceolata* Burck or *Shorea parvifolia* Dyer) that were common throughout the experimental site were chosen. *Dryobalanops lanceolata* is restricted to Borneo and is by far the commonest Dryobalanops in North Borneo (Meijer and Wood, 1964). However, due to the increased demand for its timber in the export trade it is listed as an endangered species (IUCN, 2008). Seedlings are generally abundant and well adapted to low and high light conditions (pers. observ.) Following timber density classification *Dryobalanops lanceolata* is described as a Medium Hardwood (Newman et al., 1998). Both *Shorea parvifolia* and *Dryobalanops lanceolata* were reported as ectomycorrhizal (Ingleby et al., 1998, Palmiotto et al., 2004). *Shorea parvifolia* is a common species throughout Peninsular Malaysia, Sumatra and Borneo. It is one of the most commonest forms of the Red Seraya group and important for its timber (Meijer and Wood, 1964). It is known as a strong light demander and seedlings are fast-growing, particularly in increased light conditions (Appanah and Weinland, 1993).

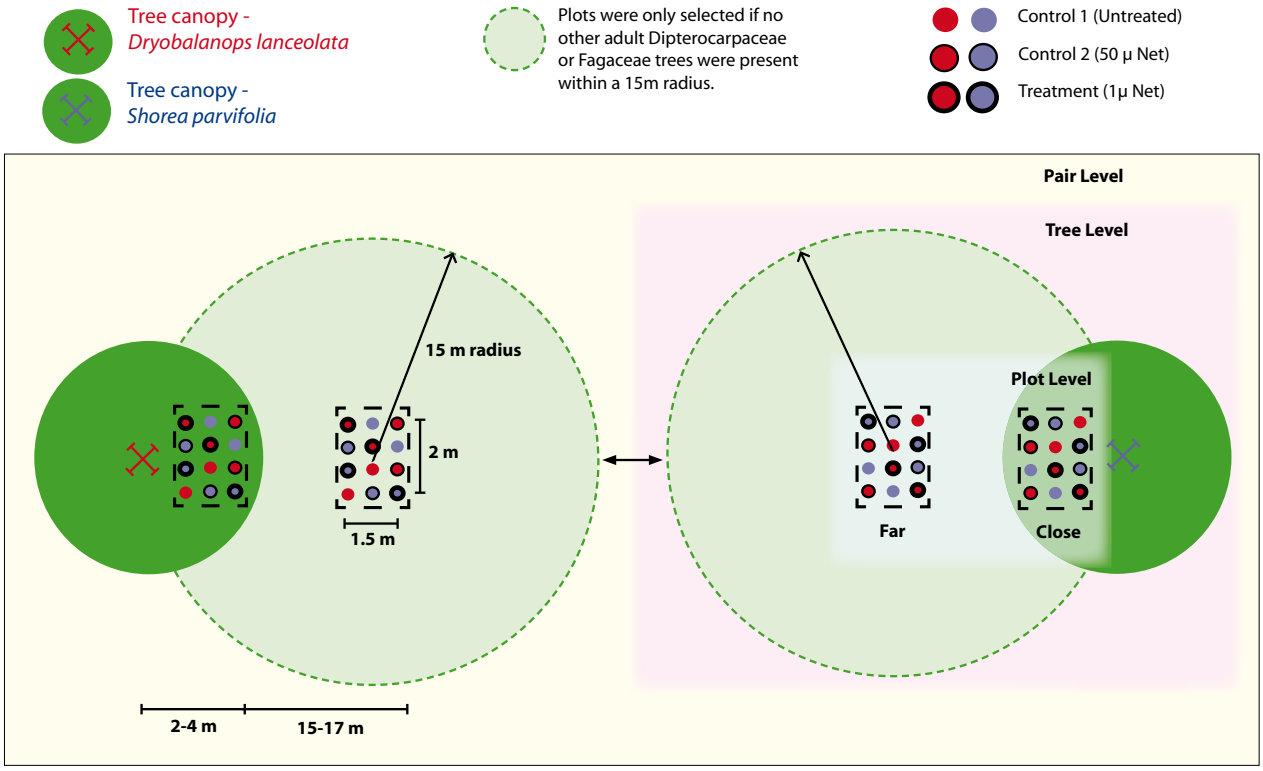


Figure 23 Description of the experimental design. One pair (Pair Level) of focal trees (*Dryobalanops lanceolata* (brown cross); *Shorea parvifolia* (blue cross) and their canopy range (green) are shown. Seedlings of both species were planted in Close or Far proximity from the focal trees (Tree Level). Two replications of all treatments (Untreated, 50 µm Net, 1 µm Net) were planted for seedlings of both species (Plot Level).

Finding isolated trees of the two species under study that would meet the criteria of our experimental design was the most challenging part. Nevertheless it allowed us to test for the effect of specificity of two members of the Dipterocarpaceae. Trees were only selected if the focal tree was the biggest tree and no other adult dipterocarp or Fagaceae trees were within 15 m distance of the experimental plots to ensure that the ectomycorrhizal network of the focal tree was closest to the planted seedlings (Fig.23). The two closest adult trees of both species were taken as a pair to control for spatial variability, whereby the distance between the pairs (60 – 400 meters) was determined with a handheld GPS (GPSMAP 60 CSx, Garmin, USA) (Table 1). At every focal tree, we planted seedlings in one plot under the tree canopy (2 – 4 m away from the stem) and in one plot outside the tree canopy (15 – 17 m away from the stem),

assuming that the tree canopy approximately reflected the range of the rooting system (Katayama et al., 2009, Baillie and Mamit, 1983). The plot effect therefore allowed us to separate the effect of the focal tree compared to the surrounding trees on the planted seedling performance. Plots (1.5 x 2 m) were carefully cleared of undergrowth prior to planting to ensure that the light levels in the plots were only artificially increased as little as possible. Light interception, defined as the percentage of canopy openness at the plot level was measured at the beginning (07/09/2006), middle (27/01/2007) and end (07/08/2007) of the experimental phase, using a Spherical Densiometer Model A (Lemmon, USA) (Table S7). We did not remove the litter layer to ensure that the existing fungal system was disturbed minimally (Brearley, 2003). To ensure a fully factorial design we planted seedlings of the species of the focal tree (conspecific) and the species of the other tree (heterospecific) in every plot. Two replicates of seedlings were planted either directly into the soil (CONTROL 1; unmanipulated control), into a PVC-pipe (70 x 15 cm) covered at the bottom with 50 µm pore size net (CONTROL 2; "pipe control" to assess pipe effects but allowing the hyphae to grow into the pipe) or 1 µm pore size net (TREATMENT; excluding the hyphae). The net-sizes were chosen because ectomycorrhizal hyphae have a diameter of approximately 35 µm and could therefore grow through CONTROL 2 but not through the TREATMENT net (Brearley, 2003). The net (SEFAR PETEX) was made of monofilament PET, which was not susceptible to biotic degradation but would allow sufficient water exchange between the pipe and the below soil. In retrospect the net proved to be less prone to the extreme environmental conditions than assumed, possibly due to the lack of an extensive soil macrofauna in tropical regions. The net was glued between the bottom of the PVC pipe and an additional PVC ring (5 x 15 cm) with silica and the PVC pieces were further adhered with aluminium tape (Appendix).

Seedlings were raised in the nursery for approximately half a year (50 cm height to apex) prior to planting in the forest and were then planted with top soil from the individual sites. They formed natural

associations with ectomycorrhiza in the nursery prior to planting (pers. observ.). Seedlings were randomly allocated to the plots and treatments, using the *sample* function in R 2.8.0 (R Development Core Team, 2008) and were planted with 0.5 m spacing in between. Seedlings were non-destructively measured (height to the apex, diameter, number of leaves) prior to harvest after one year (August 2007). Their leaves, shoots, stem roots and fine roots were severed separately and oven dried at 70°C for 72 hours prior to weighing.

### 9.4.3 Statistical analysis

Of the initial 480 seedlings we used 301 (63%) for the final analysis, which was in the range of our expectations (Lee, pers. comm.). Exclusion from the analysis was a result of mammal damage (in particular pigs and elephants), insect damage of the below ground net (in particular termites and ants), water saturated PVC pipes (due to soil compaction) and tree- and branchfalls (windstorms). Manipulated seedlings were only included in the analysis if they had an intact net at the end of the experiment. Mean seedling mass was calculated over the two replicates at the plot level, however, since for some of the treatments both replicates were missing we included 222 out of 240 possible observations in the final analysis. A heavy wind storm caused an immediate increase in light at the start of the experiment in some of the plots. As a result, PAIR number 1 (n = 28), 3 (n = 46) and 8 (n = 38) were excluded from the analysis (Table S7). For the final analysis we selected only tree pairs with mean light interception <6% across the plots (n = 7) (Table S7). This was to ensure that only seedlings were included that were exposed to low light levels and therefore would benefit from support of the ectomycorrhizal network.

We used the *lme* function implemented in the *nlme* package (Pinheiro and Bates, 2000) in R 2.8.0 (R Development Core Team, 2008) since our experimental design included fixed and random effects and was unbalanced. We checked for normally distributed residual errors during analysis. Tree species

(*Dryobalanops lanceolata* or *Shorea parvifolia*), proximity (CLOSE or FAR), specificity (CONSPECIFIC or HETEROSPECIFIC) and treatment (CONTROL 1, CONTROL 2, TREATMENT) were treated as fixed factors. Tree PAIR (n = 7), individual TREES (n = 14) and PLOTS (n = 28) were treated as random terms. Estimates of initial seedling mass were derived from non-destructive (basal diameter, height to the apex, number of leaves) measures using allometric equations and included into the model as a size correcting covariable. We present initial size-corrected relative growth rate (RGR) of height to the apex (cm) and total mass (g) (Hunt, 1990).

$$RGR = \frac{\log_e {}_2W - \log_e {}_1W}{{}_2T - {}_1T} \qquad (10)$$

Relative growth rate (RGR) is calculated as the change in log mass over time ($_2T$-$_1T$). In our case initial size was particularly important when analyzing relative mass growth, whereby height growth was not affected significantly.

Model selection was based on Akaike information criterion (AIC), assessing the importance of every term by fitting the model with and without it using the anova function, whereby the best model was selected based on the lowest AIC. When there was no clear best model ($\Delta$ AIC < 10 units) we present the simplest model (Burnham and Anderson, 2004).

## 9.5 Results

### 9.5.1 Size-corrected relative growth rate of height

The pipe significantly decreased the mean relative height growth of seedlings (Mean difference of -0.00030 cm cm$^{-1}$ day$^{-1}$; with 95% CI = -0.00055 to -0.00004 between CONTROL 1 and CONTROL 2). In both treatments with pipes, seedlings planted with 1 µm net (TREATMENT) did not grow significantly less in height (Mean difference of -0.000004 cm cm$^{-1}$ day$^{-1}$; with 95% CI = -0.00026 to 0.00026) than seedlings

with 50 µm net (CONTROL 2). Proximity to the mature tree for average over treatment (Δ AIC = 8.3) had a minor influence on relative seedling height growth whereby seedlings far from the mature tree grew not significantly less in height compared to the ones closeby (Mean difference of -0.00085 cm $cm^{-1}$ $day^{-1}$; with 95% CI = -0.00203 to 0.00032). We found a strong interaction between mature tree species and specificity of the seedlings. Averaging over models (Δ AIC = 3.0) indicated that *Shorea parvifolia* seedlings grew significantly worse when associated with a mature tree of its own species than of the other species (Mean difference of -0.00046 cm $cm^{-1}$ $day^{-1}$ with 95% CI from -0.00078 to -0.000132). In contrast *Dryobalanops lanceolata* seedlings grew significantly better under a mature tree of its own species compared to the other species (Mean difference of 0.00040 cm $cm^{-1}$ $day^{-1}$ with 95% CI from 0.00005 to 0.00075) (Fig.24).

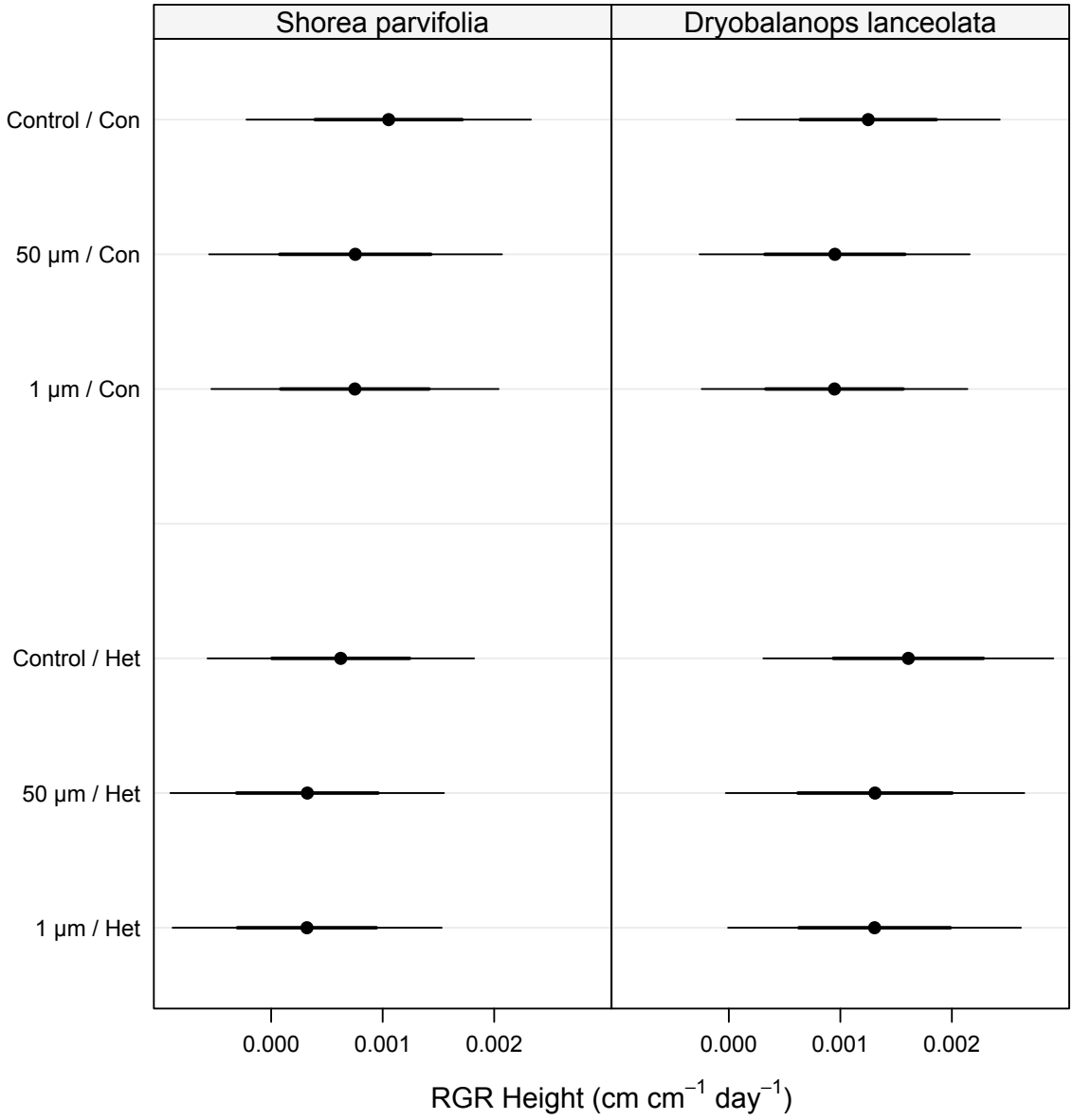


Figure 24 Mean (± SEM and 95% CI) relative growth rate (RGR) of seedling height. Note that credibility intervals include the variation from the random variables and are therefore not suited to depict significant differences. *Shorea parvifolia* seedling relative growth near a mature tree of the same species (top left half) and of the other species (bottom left half). *Dryobalanops lanceolata* relative seedling growth near a mature tree of the same species (top right half) and of the other species (bottom right half). Control represents the seedlings planted without the pipe (CONTROL 1). 50 µM stands for seedlings planted within the pipe but allowing the ectomycorrhizal network to connect (CONTROL 2). 1 µm stands for exclusion of the ectomycorrhizal network (TREATMENT). Con: Conspecific, Het: Heterospecific.

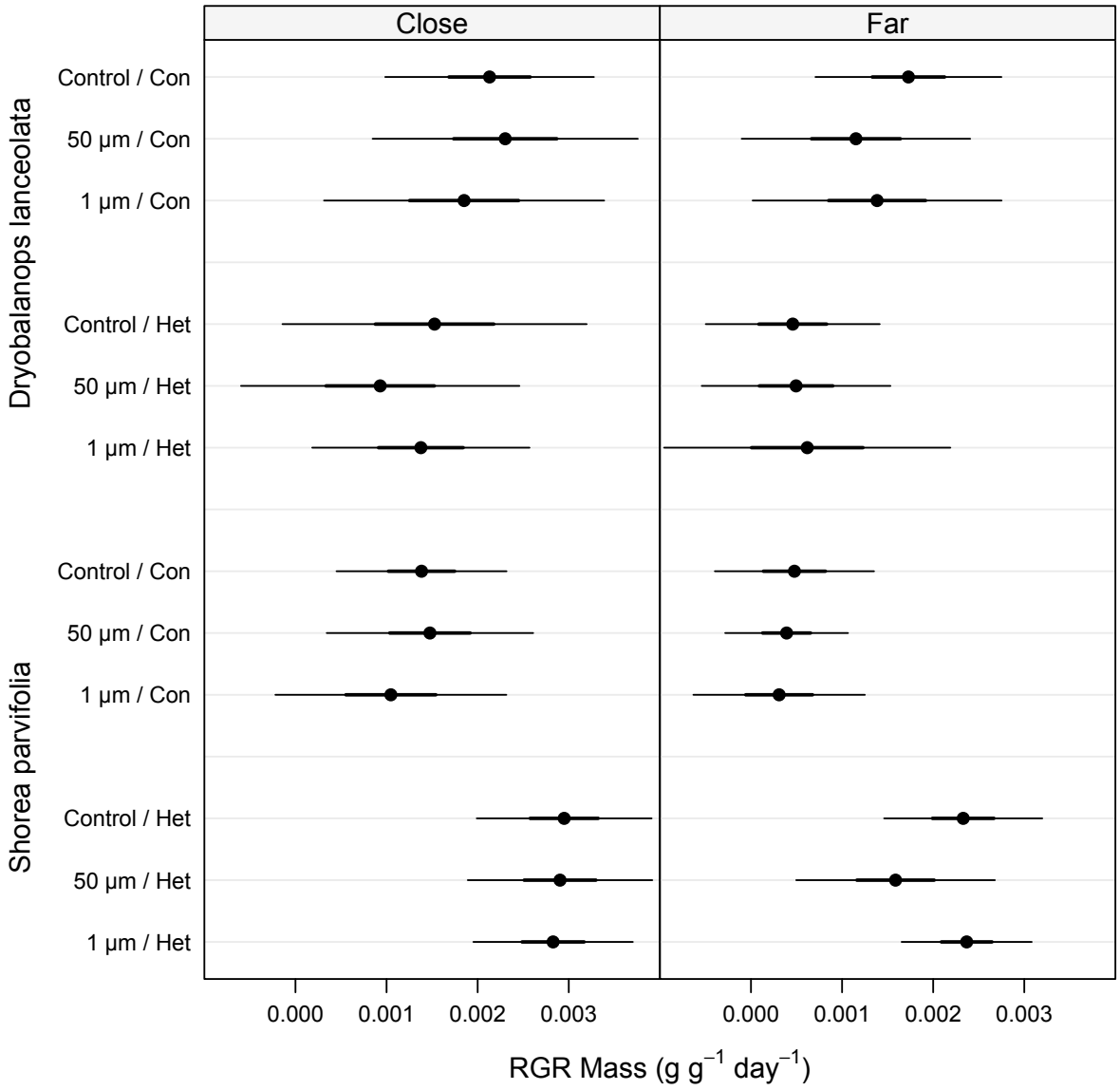


Figure 25 Initial size-corrected average (Mean ± SEM and 95% CI) relative growth rate of total seedling mass. Note that credibility intervals include the variation from the random variables and are therefore not suited to depict significant differences. *Dryobalanops lanceolata* relative seedling growth (top half) and *Shorea parvifolia* (bottom half) are shown. Control represents the seedlings planted without the pipe (CONTROL 1). 50 µM stands for seedlings planted within the pipe but allowing the ectomycorrhizal network to connect (CONTROL 2). 1 µm stands for exclusion of the ectomycorrhizal network (TREATMENT). Con: Conspecific, Het: Heterospecific. Proximity to mature tree is either Close or Far.

### 9.5.2 Size-corrected relative growth rate of mass

Contrary to relative growth of height, the pipe did not significantly decrease relative seedling mass growth (Mean difference of -0.00025 g $g^{-1}$ $day^{-1}$ with 95% CI = -0.00070 to 0.00020 between CONTROL 1 and CONTROL 2). Further seedlings planted with 1 µm net (TREATMENT) did not grow significantly less (Mean difference of -0.00005 g $g^{-1}$ $day^{-1}$ with 95% CI = -0.00052 to 0.00041) in mass than seedlings with access to the ectomycorrhizal network (CONTROL 2). The findings suggest that in terms of mass accumulation neither the pipe nor the ectomycorrhiza-seedling connection altered the seedlings relative growth rates. We did find that seedlings grew significantly better close to the mature tree (Mean difference of 0.00085 g $g^{-1}$ $day^{-1}$ with 95% CI = 0.00002 to 0.00168) compared to the ones further away. In agreement with the growth analysis of height we found again a strong interaction between mature tree species and specificity of the seedlings. When averaging over models (Δ AIC = 0.1) seedlings under a mature *Shorea parvifolia* grew significantly better when heterospecific (Mean difference of 0.00191 cm $cm^{-1}$ $day^{-1}$ with 95% CI from 0.00135 to 0.00245) whereas close to a *Dryobalanops lanceolata* mature tree seedlings grew significantly worse when heterospecific (Mean difference of -0.00122 cm $cm^{-1}$ $day^{-1}$ with 95% CI from -0.00176 to -0.00067) (Fig.25).

## 9.6 Discussion

To date, several studies have addressed the benefits to seedlings of being in contact with living roots from trees of the tropics (Alexander et al., 1992, Smits, 1994, Yasman, 1995, Newbery et al., 2000). However, only few have tested the direct benefit of an ectomycorrhizal network under field conditions (Onguene and Kuyper, 2002, McGuire, 2007, Brearley, 2003). Out of these there is only one study on Dipterocarpaceae, and this study could not detect significant interactions in growth between treatments (Brearley, 2003). On the basis of studies with net-bound seedlings and root trenching he revealed no importance of an ectomycorrhizal network for seedling establishment of *Parashorea tomentella* or *Hopea nervosa*. In con-

trast the two published studies on the influence of ectomycorrhizal networks for seedling establishment in the tropics (McGuire, 2007, Onguene and Kuyper, 2002) reported a significant increase in mass growth (35%) and in height growth (31%) respectively. Despite their large geographical separation (Cameroon and Guyana) both studies were done on Caesalpiniaceae, which shows similar ecological adaptations compared to the Dipterocarpacae. Both families form a monodominant rain forest comprising up to 70 – 90% of the canopy and exhibit irregular mast fruiting events (Henkel, 2003). Comparing the existing studies would therefore provide some evidence that the support of seedlings through an ectomycorrhizal connection may exist for Caesalpiniaceae but not for Dipterocarpaceae. However, besides the ecological similarity of the study families we found differences regarding the methods of the studies involved. A constraint in all four studies is that they did not directly test for a network association. Even though seedlings were reported to be associated with ectomycorrhiza, this does not imply the relevance of the ectomycorrhizal network. Labelling studies may therefore be a more promising technique to untangle the importance of an ectomycorrhizal network on growth of seedlings (Högberg et al., 1999).

Further, we presume that the studies differed with respect to light levels, which is known to be highly heterogenous in the understorey of tropical rain forests (Chazdon and Pearcy, 1991, Bungard et al., 2002, Leakey et al., 2004). We could not find any values for reported light levels in any of the tropical studies on ectomycorrhizal networks. However low light conditions are a prerequisite if we assume that seedlings exposed to the below light compensation point are nursed by mature trees. If light is abundant the carbon transfer from the parent tree to the seedling over an ectomycorrhizal network may not be crucial and the seedling could act as a source rather than a sink. Bungard et al. (2002) reported understorey light levels in secondary dipterocarp lowland forests to be approximately 20% higher than in primary forest understorey. In the present study light interception was similar for mature Dryobalanops lanceolata in close (Mean ± SEM; 4.9 ± 1.3) and far (2.6 ± 0.8) proximity compared to Shorea parvifolia (close: 4.3 ± 1.4;

far: 3.4 ± 1.1). Dipterocarps and in particular the heavy hardwood species are known to persist in the understorey for years, whereby particular sunflecks may compensate for low light conditions if understorey plants can respond to excess light (Watling et al., 1997). Eschenbach et al. (1998) measured light compensation points between 6-8 µmol $m^{-2}$ $s^{-1}$ for dipterocarps (including *Dryobalanops lanceolata*) whereby an irradiance of 5-20 µmol $m^{-2}$ $s^{-1}$ below the canopy is about 1% full sunlight. The study seedlings of the two species are known to respond differently to low light levels. *Dryobalanops lanceolata* is an expected generalist and performs well under all light conditions including low light and nutrient levels, whereas *Shorea parvifolia*, similar to *Shorea johorensis* is light and nutrient demanding (Bungard et al., 2002). Both species responded similarly to the experimental treatments, suggesting that seedlings of both species could maintain a positive carbon balance throughout most of the experiment.

In our study ectomycorrhizal morphotypes on planted seedlings were naturally formed in the nursery and could have differed from the late-successional species found in the field (Jones et al., 2002, Jones et al., 2003). However, we assume that an experimental duration of one year was long enough for the seedlings to form ectomycorrhizal associations with fungi associated in mycorrhizal networks, which typically takes approximately three months (Lee, pers. comm.). A further constraint was that we tested for relative seedling growth in height and mass, but not for survival. We chose an experimental duration of one year since we had to trade-off between prolonging the experiment to measure the proposed effect and harvesting the seedlings to achieve enough replication. During the experimental phase seedling survival was mostly determined by external factors such as mammal damage (in particular pigs and elephants), water saturated PVC pipes (due to soil compaction), tree- and branchfalls (windstorms) and could not be directly related to a possible effect of the mycorrhizal network.

Irrespective of experimental treatments, seedlings of *Dryobalanops lanceolata* and *Shorea parvifolia* grew better when associated with mature *Dryobalanops lanceolata* trees. Further, seedlings grew better in mass

in close proximity to the mature tree. Together these patterns may suggest that species-specific traits were important for height and biomass accumulation of seedlings growing in low light conditions. Soluble carbohydrates in the soil matrix of the rooting zone could be directly absorbed by the seedlings growing near the focal trees, implying that carbon transfer through the soil pathway is more relevant for seedling growth (Robinson and Fitter, 1999). Hence decreases of soluble carbohydrate concentrations further away from the mature tree may explain the found proximity effect, however we could not provide direct evidence for this assumption. In particular soil animals (collembola, earthworms) which feed on hyphae of the mycorrhizal fungi may disrupt the carbon transfer over the mycorhizal network. Voets et al. (2008) argue that even if carbon is translocated from a donor to a receiver plant via the fungal network, it is not yet confirmed that the carbon is really transferred to the receiver' plant tissue and does not remain in the intraradical fungal structures. Hence, more complex methods to determine carbon flows were proposed whereby accurate quantification of belowground carbon movement still remains unclear due to methodological problems such as pulse level size or the choice of carbon isotope $^{13}C$ or $^{14}C$ (Philip and Simard, 2008).

In conclusion we found no evidence for the importance of an ectomycorrhizal network that supported Dipterocarpaceae seedling growth in understorey light conditions. Further, we could not support the hypothesis that a conspecific stand is beneficial since seedlings of both species grew better in proximity of mature *Dryobalanops lanceolata* trees. A simple explanation may be that mature *Dryobalanops lanceolata* are mainly located in favorable spots for seedling growth, namely in flatter parts compared to steep hills with leached soil. Proximity to a mature tree affected the growth in height and mass of seedlings marginally, suggesting that tree specific traits such higher concentrations of soluble sugars within the rooting zone may favor seedling growth. The importance of carbon transfer to seedlings is a controversial area

(Newbery et al., 2000) and more convincing experimental evidence is required to draw further conclusions about its role in tropical forests (Alexander and Lee, 2005).

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# 9.8 Appendix

Table S7 Overview of tree (SP: *Shorea parvifolia*, DL: *Dryobalanops lanceolata*) and plot characteristics. Pair 1, 3, 8(*) were excluded from the analysis due to high light interception values in some of the plots (PAR >12%)

| Pair | Distance | Tree | DBH | Elevation | Close Proximity | Distant |
|---|---|---|---|---|---|---|
| | m | Species | cm | m | PAR (%) | PAR (%) |
| **1*** | 138 | SP | 78.0 | 161 | 21.3 | 12.9 |
| | | DL | 80.5 | 133 | 2.3 | 15.3 |
| **2** | 169 | SP | 76.1 | 135 | 6.9 | 1.8 |
| | | DL | 43.9 | 130 | 6.8 | 1.8 |
| **3*** | 300 | SP | 69.4 | 228 | 1.5 | 1.6 |
| | | DL | 74.5 | 195 | 13.9 | 4.7 |
| **4** | 57 | SP | 60.2 | 226 | 1.3 | 1.9 |
| | | DL | 38.5 | 178 | 2.2 | 1.3 |
| **5** | 301 | SP | 60.2 | 163 | 3.8 | 2 |
| | | DL | 83.0 | 186 | 1.8 | 1.3 |
| **6** | 147 | SP | 53.5 | 138 | 1.8 | 3.8 |
| | | DL | 97.1 | 143 | 2.3 | 6.5 |
| **7** | 400 | SP | 50.9 | 176 | 11.1 | 2.3 |
| | | DL | 82.1 | 143 | 8.6 | 1.5 |
| **8*** | 113 | SP | 71.0 | 156 | 20.3 | 29.4 |
| | | DL | 58.6 | 156 | 8.2 | 1.5 |
| **9** | 104 | SP | 79.6 | 152 | 4 | 9.7 |
| | | DL | 82.4 | 134 | 2.9 | 1.8 |
| **10** | 205 | SP | 83.1 | 148 | 1.3 | 2.3 |
| | | DL | 71.6 | 160 | 9.5 | 4.2 |

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# 10 General Discussion

Enhancing existing carbon stocks through forest management practices is one option to increase productivity in logged forest, as it will remove carbon dioxide ($CO_2$) from the atmosphere that was released by logging through sequestration of carbon in trees (Murray, 2009). This has potential market value, as carbon credits can be traded between those who sequester carbon and the producer of $CO_2$ emissions. To date forest management practices in developing and emerging nations are not included in the carbon trading scheme of the CDM (Clean Development Mechanism) under the Kyoto protocol (Michaelowa and Dutschke, 2009). The reason is that both, the EU and environmental NGOs perceive forest climate mitigation in developing countries as an excuse for industrialized countries to avoid "more serious" mitigation action (Michaelowa and Dutschke, 2009). In addition they argue that forest management in developing countries may encourage the conversion of native ecosystems to non-native forest plantations, undermining biodiversity and water resource provision, so called perverse incentives (Jackson et al., 2005). This decision affected forest rehabilitation efforts in developing countries for the last decade, but is likely to be overthrown at the COP–15 (Conference of the Parties) of the United Nations in Copenhagen, 2009 (Koh et al., 2009). The agreements will also determine the role of forest management for the post-Kyoto (after 2012) climate change regime. Firm decisions are urgently needed since deforestation is continuing at an alarming rate, for example most recent estimates (2003–2008) for Borneo predict that at the current pace no lowland mixed dipterocarp forest will remain after 2020 (M. Radday, pers.comm.). On the basis of such future development it is essential to better understand the most effective practices of sustainable forest management in developing and emerging nations. In Chapter 1 we introduced a large scale forest rehabilitation project–the Sabah Biodiversity Experiment–dedicated to contribute to our knowledge of how forest rehabilitation with native trees of a diverse mixture may affect fundamental ecosystem processes (Saner et al., 2009). The findings of this long term experiment are of particular interest to the carbon credit market as more evidence will aid potential investors to quantify the multiple benefits that forest

rehabilitation of degraded forests in the tropics has to offer (Barlow et al., 2007). If tree diversity provides an additional market value for carbon credits this may become a strong incentive for investors interested in emission reductions from sustainable forest management, such as reduced impact logging, enrichment planting and forest restoration or forest conservation projects (Grace, 2004, Kitayama et al., 2006). An eventual study should therefore relate productivity and ecosystem multifunctionality for the logged forest under study. In this thesis we simultaneously considered both, a baseline carbon and tree diversity estimation for 30 year old logged forest (Chapter 2) that provides initial measurements for future studies. We found that the forest shows depleted levels of carbon stocks compared to undisturbed forest and that intervention is needed to re-stock the forest with native dipterocarp trees (Chapter 2). Studies of the tree diversity suggest that the 500 ha area of the Sabah Biodiversity Experiment could also maintain local tree diversity (Chapter 2), it is therefore important to consider the background vegetation from a conservation perspective (Ashton, 2008). Despite the lack of the dominant dipterocarp trees in the background vegetation, our findings indicated that the 30 year old logged forest of the Sabah Biodiversity Experiment can fully maintain some ecosystem carbon turnover rates. In particular quantity of dead standing wood, fine root biomass and litterfall rates were found to be similar to reported values of unlogged forest (Chapter 2). In contrast soil respiration rates (Chapter 3) were found to be higher in our study (28.6 ± 1.2 Mg C $ha^{-1}$ $yr^{-1}$ SEM), than reported values from Pasoh Forest Reserve in West Peninsular Malaysia (14.2 Mg C $ha^{-1}$ $yr^{-1}$) (Kira 1978) or more recent estimates from Lambir, Sarawak (21.6 ± 1.4 Mg C $ha^{-1}$ $yr^{-1}$) (Katayama et al., 2009). On the basis of our results from logged forest (Chapter 2 and 3) we present a first general carbon budget for the Sabah Biodiversity Experiment (Fig.26).

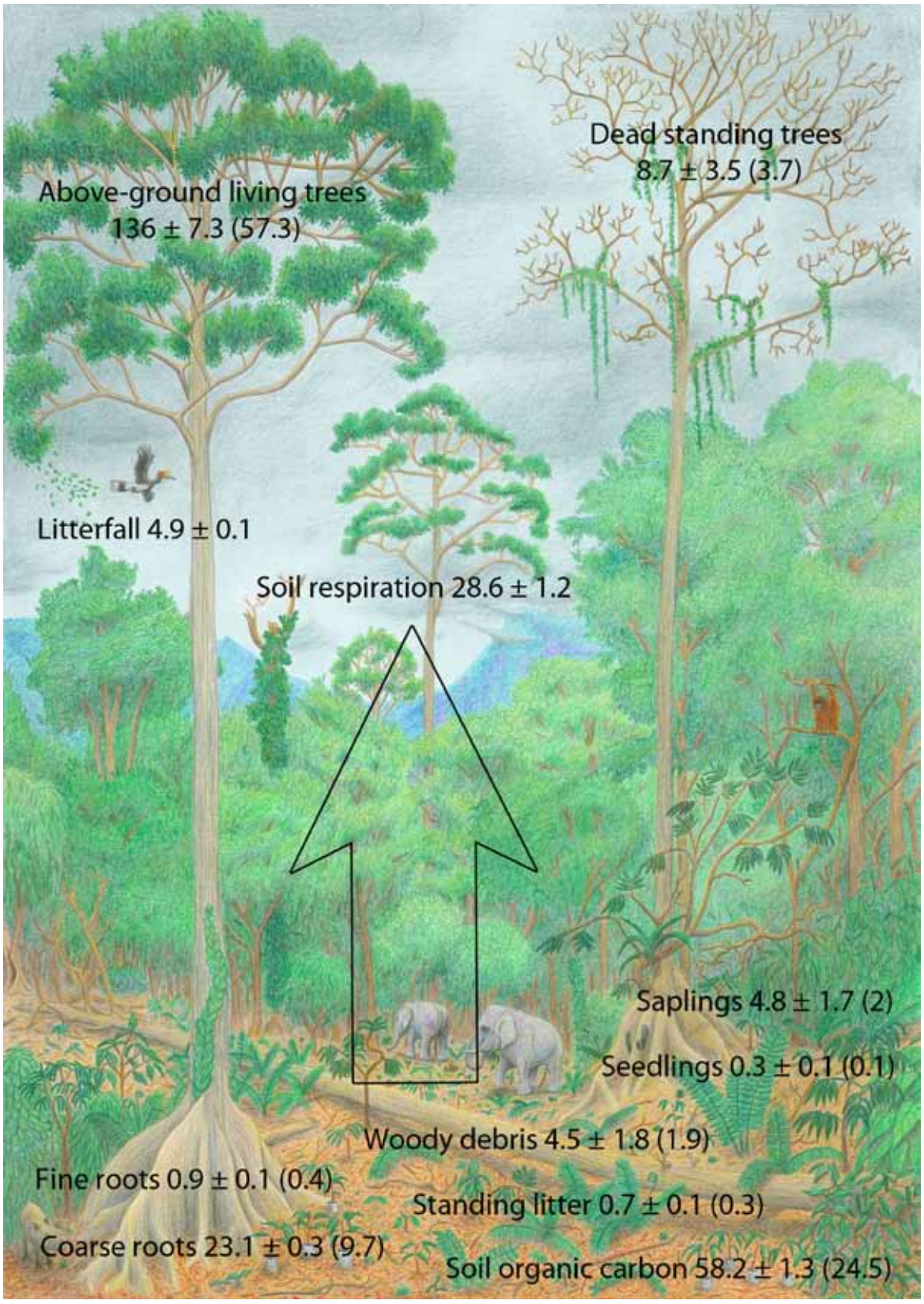


Figure 26 General carbon budget for the background vegetation of the Sabah Biodiversity Experiment. All estimates are given in Mg C $ha^{-1}$ (Mean ± SEM). Values in parenthesis indicate the percentage of single carbon stocks to total organic carbon (237.2 ± 8.4). Carbon flux estimates (litterfall and soil respiration rates) are reported as Mg C $ha^{-1}$ $yr^{-1}$. For details on the methods see Chapter 2 and 3.

Future research towards a comprehensive carbon budget for the Sabah Biodiversity Experiment should determine tree biomass increase and whole ecosystem respiration to infer forest productivity. One of the first estimates of primary productivity for humid tropical forests of Malaysia was summarized by Kira (1978). For Pasoh Forest Reserve in West Peninsular Malaysia they estimated tree (DBH ≥ 4.5 cm) biomass increase at 5.3 Mg $ha^{-1}$ $yr^{-1}$, above-ground net production rate at 21.2 Mg $ha^{-1}$ $yr^{-1}$ and the primary production at 25.7 Mg $ha^{-1}$ $yr^{-1}$. Initial tree biomass of their study (431 Mg $ha^{-1}$) was similar to our estimates of unlogged forest at Danum Valley (Chapter 2: 469 ± 74 Mg $ha^{-1}$ SEM). It is expected that the net primary production of the logged forest of the Sabah Biodiversity Experiment is higher, as the forest is younger with lower biomass stores and therefore growing faster (Kira, 1978). For general predictions of biomass increase of the Sabah Biodiversity Experiment we suggest using the growth and yield estimates from a six year survey derived from a logged forest located in the Kalabakan Forest Reserve (Udarbe, 1995). Timber volume extraction (11 trees > 60 cm DBH, 80 $m^3$ $ha^{-1}$), total stocking of dipterocarps (27% of total basal area), geology (Kalabakan Formation), soil parent material (mudstone and sandstone) and landform (moderate to high hills) were similar to the area of the Sabah Biodiversity Experiment (Chapter 1). The yearly mortality rate for trees >10 cm DBH was reported at 5% ± 1.7% SEM, where the mortality occurred mainly in the 10-20 cm DBH class (47%). Tree diameter increment was reported at 0.68 ± 0.03 cm $yr^{-1}$ for dipterocarps and at 0.61 ± 0.11 cm $yr^{-1}$ for non dipterocarps (Udarbe, 1995). The best models available to date for predictions of biomass increase in logged forest are FORMIND and FORMIX3 (Huth, 2009) and CO2FIX V 3.1 for quantifying carbon sequestration (Schelhaas et al., 2004). We suggest incorporating the data of our study into more extensive research on the fundamental relationship between carbon storage and tree diversity for the lowland mixed dipterocarp forests of Borneo, including studies from primary forest, logged forest, fragmented forest areas and oil palm (*Elaeis guineensis*) plantations.

Our results (Chapter 2) suggest that rehabilitative measures are indeed needed to regain the carbon storage potential of the logged forest. In the case of the Sabah Biodiversity Experiment the technique of enrichment planting was chosen, where dipterocarp seedlings are planted along previously opened lines into the existing logged forest (Chapter 1). In a comprehensive review of practices in sustainable management of Malaysian rainforest Appanah (2001) states that in retrospect enrichment planting turned out to be unreliable from a forestry perspective, in particular since the forest must be kept open for at least 8–10 years for the seedlings to establish and enter the growth phase. If this is not applied the canopy will close after one year and the seedlings will not grow. Preliminary data from the Sabah Biodiversity Experiment indicates that line enrichment planting may be susceptible to high (>50%) initial seedling mortality for the first five years after planting, most likely due to reduced amount of lateral light available to seedlings (Bebber et al., 2002) and subsequent susceptibility to mammal damage. Patch planting into artificial gaps or the selective liberation of potential crop trees by removal of overhead shade and cutting of vines and climbing bamboo may be a promising alternative for rapid increases in timber stocks from a forest management perspective (Romell et al., 2008).

As light is a driving factor for seedling establishment we were interested to study the ecology of selected dipterocarp species that are used as the planting stock for forest rehabilitation under altered light environments. Dipterocarp growth was shown to be influenced by light and the allocation of photosynthates in the establishment phase (Chapter 4). We used a novel approach to analyze seedling growth as a power function of mass, where the mass scaling exponent ($\beta$) was estimated at 0.67 and therefore close to the two-thirds exponent of biomass growth for plant communities of the Kleiber's law and the three-quarter law proposed by West et al. (1997). We compared the expected mass predicted by the growth model under constant light conditions to observed mass after simulating canopy gap formation and closure. We found a trade-off between the allocation of resources to either growth or storage of non-structural

carbohydrates in five out of six dipterocarp species (*Dryobalanops lanceolata, Hopea nervosa, Shorea argentifolia, Shorea macroptera, Shorea parvifolia*, but not for *Shorea leprosula*). This indicates that total amounts of non-structural carbohydrate is an important trait to consider, as depletion could determine seedling survival under sub-optimal conditions (e.g. low light, herbivory, water stress, nutrient deficiency) and a growth versus survival trade-off may play a role in explaining tree species coexistence in tropical forests. In addition our results suggested that carbon stored in dipterocarp seedlings as non-structural carbohydrates are present in the form of starch and soluble sugars. Separating the soluble sugar components according to their complexity revealed that simple sugars, in particular sugar alcohols (polyols) were a major contributor to total non-structural carbohydrates. We identified Iditol as a sugar alcohol that–according to our knowledge–has not been reported in tropical trees before. Although its function remains unclear in dipterocarps it has been shown from other studies (Holmstrom et al., 1996) that polyols are relevant for stress tolerance. We therefore suggest that future studies on dipterocarps should specifically address how polyols are related to stress such as drought tolerance (Choat et al., 2007), or nutrient deficiency and the plausible role of associated ectomycorrhiza.

Carbon that is stored in plants through the process of photosynthesis is further allocated to structural tissue, to non-structural carbohydrates or may be used to support associated ectomycorrhiza (plant-fungi-symbiosis). Based on this premise we argued that the relative value of stored carbon is potentially dependent on light conditions and that it may be more advantageous to trade carbon for nutrients with ectomycorrhiza under low light than high light (Chapter 5). We therefore expected a negative relationship between seedling growth and ectomycorrhizal infected root tips in the dark understorey. Our results reject this hypothesis for *Vatica albiramis* (Dipterocarpaceae) as the positive relationship between ectomycorrhizal infection and seedling growth was consistent across three forest floor light levels (understorey, small and large gap). Both experimental shadehouse studies (Chapter 4 and 5) consider fundamental factors

that control plant growth and hence carbon storage. However, for both experiments we found that dipterocarp seedlings were not exposed to their below-light compensation point (Eschenbach et al., 1998) as they were still growing in the dark. For future studies on proposed life history trade-offs between survival in the dark and growth in the light we therefore suggest to use lower light conditions (e.g. four layers of 70% shade cloth).

Our results (Chapter 5) indicated that ectomycorrhizal association can be maintained on dipterocarp seedlings growing in a light constrained environment. Hence it could be expected that adult dipterocarp trees may nurture seedlings that grow below the light compensation point through a mycorrhizal network that connects both (Teste and Simard, 2008). Such evidence would support positive density dependence, where seedlings located close to the mother tree grow better than the ones further away (Chapter 6). This is in contrast to proposed negative density dependence, which assumes that an increased seed and seedling predation close to adult trees may drive tree species coexistence (Hautier et al., in prep.). Seedlings grew better close to adult trees of *Dryobalanops lanceolata*, however the increased growth could not be related to the proposed connection to a local ectomycorrhizal network for *Dryobalanops lanceolata* and *Shorea parvifolia* seedlings. Despite limited evidence for the importance of ectomycorrhiza for tree species coexistence we suggest that future studies should further reveal the effect of the background vegetation on dipterocarp seedling performance, for example through the effect of spatially explicit neighbourhood data on experimentally planted dipterocarp seedlings (Uriarte et al., 2004).

The experimental work presented here advances our knowledge on potential niche axes of selected dipterocarp species which is needed to test whether random (neutral) processes can explain tree species diversity in tropical forests.

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# 12 Curriculum Vitae

PERSONAL

| | |
|---|---|
| Name | SANER |
| First name | Philippe |
| Date/City of Birth | 25th November 1978 in Beinwil (SO) |
| Nationality | Swiss |

EDUCATION

| | |
|---|---|
| High school | Lyceum Alpinum Zuoz, Switzerland 1991 – 1998 |
| University: | University of Zürich, Switzerland 2000 – 2009 |
| Diploma Degree | Biology with main subject in Zoology and minor subject in Microbiology and Environmental Sciences, 2000 – 2003 |
| Diploma Thesis | Institute of Environmental Sciences, University of Zürich, Switzerland, 2004 – 2005<br>"Does the growth performance of dipterocarp saplings follow an ecological trade-off?"<br>Supervisor: Prof. Dr. Andrew Hector |
| PhD Thesis | Institute of Environmental Sciences, University of Zurich, Switzerland, 2006 – 2009<br>"Ecosystem Carbon Dynamics in Logged Forest of Malaysian Borneo"<br>Supervisor: Prof. Dr. Andrew Hector<br><br>Employed as PhD student at the University of Zurich since March 2006. |

PUBLICATION

Peer-reviewed

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A. Jumpponen, C.P.H. Mulder, C. Palmborg, J.O.S Pereira, A.S.D. Siamantziouras, A.C. Terry, A.Y. Troumbis, B. Schmid, M. Loreau. Diversity and Stability: A Multisite Test of the Insurance Hypothesis Using Experimental Grassland Communities. Ecology in revision.

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